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FATE OF TYPICAL LAKE PLANKTON IN STREAMS

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FATE OF TYPICAL LAKE PLANKTON IN STREAMS*

INTRODUCTION

The belief that a lake supports a plankton fundamentally different from that of flowing water was first expressed by Zacharias (1898) when he proposed the term *potamoplankton* to designate a definite group of plankton organisms which he believed to exist only in running water. In subsequent investigations on streams and lakes, it was claimed that there are characteristic differences between the plankton of the two situations and that these differences can be explained on the basis of contrasting environmental conditions. Knowledge concerning differences between the plankton of a stream and of a lake has been derived primarily from a comparison of results of independent investigations on each of these situations. Up to the present, it has not been demonstrated what happens to lake plankton when it is subjected to the environmental conditions of a stream. The purpose of this paper is to present the results of a study of streams without tributaries or pollution deriving water directly from a lake. In such a situation, plankton produced in a typical lake is suddenly subjected to the environmental conditions of a stream.

Work was begun in June, 1930, and continued to the spring of 1934. During this period three situations were studied. In the region of Ann Arbor, Michigan, there are two lakes, Base Line and Portage, the outlets of which unite to form a portion of the Huron River. These lakes and the succeeding five-mile portion of the river were studied continuously over a period of eighteen months, during which time two or three plankton collections were made each month. In the region of Douglas Lake, Michigan, two situations were studied, namely, Maple River, which has its source in Douglas Lake, and Bessey Creek, which has its source in Lancaster Lake. Both were investigated during the summers of 1930, 1932, and 1933. Also, in late October, 1932, and in November, 1933, work was done on Maple River. Lancaster and Douglas lakes were investigated only to the extent of determining the quality and quantity of plankton which they contributed to Bessey Creek and Maple River respectively.

During this investigation, 600 plankton samples were studied qualitatively and quantitatively. Approximately 400 were collected from Portage Lake, Base Line Lake and from that portion of the Huron River formed by the union of the outlets of these lakes. About 125 samples were taken from Maple River and 75 from Bessey Creek. In addition, numerous collections of aquatic vegetation, bottom ooze, sediment and various kinds of debris occurring in these streams were made and studied in relation to this problem. Certain physical-chemical analyses were made on each situation.

Base Line Lake (Fig. 1) is located about 18 miles northwest of Ann

* Contribution from the Department of Zoology and from the Biological Station, University of Michigan.

Arbor, Michigan. It, with Portage Lake, is at the lower end of a series of lakes lying in the upper portion of the Huron River drainage system. It is about 1 mile long and 0.7 mile wide. That part giving rise to the outlet is a narrowly constricted bay with steep sides and a maximum depth of 12 meters. The outlet is approximately 15 meters wide with an average depth of 1.5 meters.

Portage Lake (Fig. 1) located about 0.2 mile west of Base Line Lake is 2.5 miles long and about 1 mile wide. That portion of the lake used for work has a depth of 15 meters. The outlet, located at the southeastern extremity, unites with the outlet of Base Line Lake to form the beginning of the lower course of the Huron River. This has a width of about 8 meters and an average depth of approximately 1 meter.

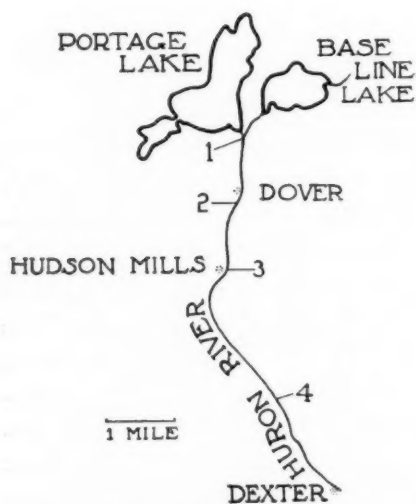


FIG. 1. Map showing Portage Lake, Base Line Lake and that portion of the Huron River between Dexter, Michigan, and union of the outlets of the two lakes. Collecting stations indicated by Arabic numerals.

Modified from the United States Geological Survey Map, Dexter Quadrangle, Michigan.

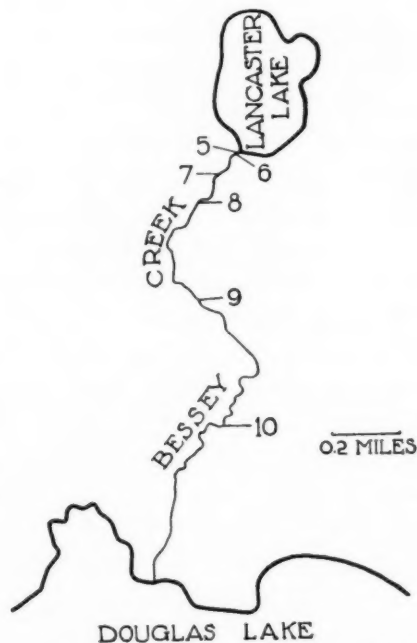


FIG. 2. Map showing Lancaster Lake, Bessey Creek and that portion of Douglas Lake into which Bessey Creek empties. Collecting stations indicated by Arabic numerals.

Modified from airplane map made by the United States Army, United States Geological Survey, and Department of Conservation, State of Michigan.

That part of the Huron River (Fig. 1) considered in this study was the portion lying between Dexter, Michigan, and the point of union of the outlets of Base Line and Portage Lakes. This section has a rather uniform course characterized by the lack of pronounced rapids or backwaters and the presence of a regular shore line. The river is free from pollution and

has no tributaries except for a few small temporary streams existing only during rainy seasons. Average current rate in this part of the river is approximately 0.4 mile per hour and does not vary greatly throughout the entire 5 miles. The water varies in width from 25 to 50 meters but the greater part of it is about 35 meters wide. Average depth is about 1.5 meters. Its substratum throughout the 5 miles is composed of mud, sand and gravel except on the riffles where stones predominate. The margins, and in many instances the entire river bed, support a copious growth of aquatic vegetation.

Bessey Creek (Fig. 2), the outlet of Lancaster Lake (Eggleton 1935), flows southward for a distance of 1.6 miles and empties into Douglas Lake. The width of the stream varies from 3 to 5 meters while the depth ranges from 15 to 18 centimeters on riffles to about 1.5 meters in pools. Rate of current is approximately 0.3 mile per hour throughout the entire course of the stream. This stream is free from pollution and has no tributaries.

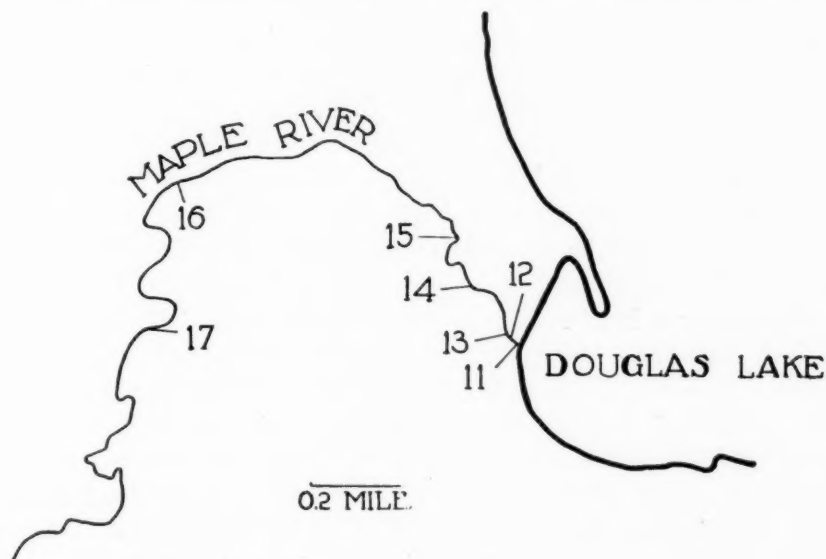


FIG. 3. Map showing a portion of Maple River and the region of the outlet of Douglas Lake. Collecting stations indicated by Arabic numerals.

Modified from airplane map made by the United States Army, United States Geological Survey, and Department of Conservation, State of Michigan.

Maple River (Fig. 3) is the outlet of Douglas Lake and empties into Burt Lake. That part considered in this work is the portion between Douglas Lake and the Bryant-Pellston road, having a length of about 1.6 miles. At the outlet of Douglas Lake, the stream is approximately 3 meters wide and about 25 centimeters deep. The entire investigated portion is free from pollution and does not have tributaries.

The writer wishes to express his indebtedness to Professor Paul S. Welch under whose direction work was done; to Professor W. R. Taylor for aid in identification of diatoms; and Professor J. H. Ehlers for assistance in

identification of certain higher aquatic plants. The assistance of many associates during this investigation is gratefully acknowledged.

METHODS AND EQUIPMENT

All temperature determinations in streams were made with a centigrade maximum-minimum thermometer, properly corrected. A Negretti and Zambra reversing thermometer was used in making temperature records in lakes.

Rate of current was measured by the float method. A bottle filled with water, until it nearly submerged, was allowed to drift a known distance. The time it took the float to travel this distance was determined with a stop watch and the rate was expressed in miles per hour. In some instances a floating cork was used.

Water samples for all chemical analyses were collected with a modified Kemmerer bottle. Hydrogen-ion concentration was determined by means of a colorimeter. Dissolved oxygen, free carbon dioxide and carbonates were determined by methods outlined in the Standard Methods for the Examination of Water and Sewage, 6th edition (1925).

All net plankton samples from streams were secured by pouring 100 liters of water through a No. 20 silk bolting cloth plankton net. In most instances, collecting stations were established at positions in the streams where water was shallow enough to wade from one shore to the other. Plankton samples from lakes consisted of 20 liters of water collected by means of a modified Kemmerer bottle. This water was also poured through a No. 20 silk bolting cloth plankton net. The concentrate from each sample was preserved immediately with formalin. Examination of plankton samples in the laboratory consisted of a qualitative and quantitative enumeration of plankters with a Sedgewick-Rafter cell and a Whipple micrometer. Concentrate of each sample was diluted to 100 cubic centimeters and mixed thoroughly until the organisms were uniformly distributed. Small and common organisms were counted in 5 cubic millimeters in each of 2 different cubic centimeters of the concentrate. The survey method was employed to enumerate the rarer and larger organisms, such as Crustacea, Rotifera and certain Protozoa, in 2 cubic centimeters of the concentrate.

STATIONS

HURON RIVER

Station 1 (Fig. 1) was located 50 meters below the point of union of the outlets of Portage and Base Line Lakes. Water at this station was approximately 40 meters wide, 1 meter deep, and the current was 0.4 mile per hour. The substratum consisted of sand, small stones and numerous clam shells coated with marl. Sparse aquatic vegetation consisted of the following species: *Chara* sp. *Elodea canadensis*, *Ceratophyllum demersum*, *Potamogeton*

pectinatus, *P. americanus*, *P. amplifolius*, *P. angustifolius*, *P. zosterifolius*, *P. Richardsonii*, and *Vallisneria spiralis*.

Plankton collections were made regularly at the outlets of Portage and Base Line Lakes in order to determine the quality and quantity of plankton each was contributing to the river. These collections were used also to show that plankton at Station 1 represented the combined plankton of the two outlets.

Station 2 was located just below the bridge at Dover, approximately 1 mile down stream from Station 1. Here, water was no more than 0.5 meter deep due to the width of the river, and the current rate was about 0.4 mile per hour. The substratum, consisting mostly of small stones and sand, supported a scant growth of aquatic vegetation.

Station 3 was established 1 mile down stream from Station 2, about 50 meters below the bridge at Hudson Mills, where the channel was about 1 meter deep and the current rate 0.8 mile per hour. This relatively swift section was only a few meters long and free from aquatic vegetation. However, above and below this station the river supported an abundance of vegetation.

Station 4 was 2.5 miles below Station 3. The water was uniformly deep, about 1.3 meters, and flowed at the rate of 0.3 mile per hour. Approximately 0.5 mile above and below this station, the substratum was composed of sand and muck which supported a dense growth of vegetation, especially during late summer.

BESSEY CREEK

Station 5 (Fig. 2) was near the outlet of Lancaster Lake where water had definitely left the lake and had become a part of the stream. Water was 3.5 meters wide and about 1 meter deep in mid-channel. The substratum consisted of an old bog mat on which a large amount of flocculent sediment and muck had accumulated. Aquatic vegetation produced a continuous bed from this station to the next one during late summer. At times of maximum vegetation the stream became nearly choked due to heavy growths of *Najas flexilis*, *Nymphaea advena*, several species of *Potamogeton* and a very profuse growth of *Lyngbya* which produced an almost continuous mat across the stream. Rate of current at this station and the succeeding one was 0.3 mile per hour.

Station 6 was 15 meters below Station 5 and at the lower edge of the vegetation bed extending between these two stations. The general features were nearly identical with those of the preceding station.

Station 7 was 0.1 mile down stream from Station 6. Here, water was very sluggish, having a width of 3 meters and a depth of 12 centimeters. The substratum consisted of sand covered with brown flocculent sediment and vegetation was absent except at the margin of the stream. Rate of current at this station and the three succeeding stations was approximately 0.2 mile per hour.

Station 8 was about 0.1 mile below Station 7 and 0.2 mile from Lancaster Lake. The water was 2.5 meters wide and no more than 13 centimeters deep. There was no vegetation for some distance above and below this station, but the stream contained large accumulations of fallen leaves and branches, especially during late summer. In several places, trees had fallen across the stream producing partial dams.

Station 9 was 0.4 mile below Station 8 and 0.6 mile from Lancaster Lake. Here, water was confined to a narrow channel with a width of 1.5 meters and a depth of approximately 13 centimeters. The channel contained several large stones covered with algae and débris. There were no higher aquatic plants at this station; however, there were heavy beds just above and below it.

Station 10 was 0.5 mile below Station 9. This section was sluggish due to the presence of numerous pools containing dense beds of vegetation. The substratum, as in other vegetated sections, was composed of muck and sand covered with a layer of flocculent sediment.

MAPLE RIVER

Station 11 (Fig. 3) was near the outlet of Douglas Lake where the water had definitely left the lake and had become a part of the stream. Here, water varied from a width of 3 meters and a depth of 20 centimeters, during early summer, to a width of 2 meters and a depth of 10 centimeters in late summer. Rate of current was about 0.4 mile per hour. The substratum was composed of flocculent marl particles washed in from the lake, forming a soft oozy bed 1 meter or more deep. This material was constantly being thrown into suspension by water currents but it settled rather quickly in the less turbulent marginal water. There was a heavy growth of vegetation, during the summer, from this station to Station 13. The predominant plants were: *Najas flexilis*, *Potamogeton heterophyllus*, *P. natans*, *Scirpus validus*, and *Chara* sp.

Stations 12 and 13 were in the same vegetation zone near the outlet of the lake, about 10 meters and 20 meters respectively, down stream from Station 11. These three stations possessed the same general characteristics.

Station 14 was 0.16 mile below Station 13. The water, which was about 3.5 meters wide and 25 centimeters deep, flowed over a uniform sand bottom free from vegetation except at the margins. Rate of current was 0.3 mile per hour. There was no vegetation above or below this station for several meters, but there were pronounced accumulations of dead leaves and débris during late summer.

Station 15 was 0.15 mile below Station 14 and approximately 0.3 mile from the lake. The water, about 5 meters wide and 20 centimeters deep, flowed at the rate of 0.4 mile per hour. A substratum of sand was free from vegetation all summer except at the margins. This section contained accumulations of leaves during late summer.

Station 16 was 0.8 mile below Station 15 and about 1.1 miles from the lake. Here, the water was 3 meters wide and 25 centimeters deep and flowing at the rate of 0.3 mile per hour. This section was partly clogged with leaves and débris but there was very little vegetation.

Station 17 was 0.5 mile below Station 16 and 1.6 miles from the lake. The width, depth and rate of current were about that of the preceding station. The sandy and stony substratum supported no vegetation.

PLANKTON DATA

HURON RIVER SITUATION

CONSTITUENT PLANKTON ORGANISMS

During this investigation, 115 species and 96 genera of plankters were identified. The complete list of plankters and a discussion of their seasonal variation will appear in another paper. Approximately 95 per cent of these plankters was the product of the lakes, the remaining 5 per cent was the product of the river. These were distributed among the plankton groups as follows:

<i>Phytoplankton</i>	<i>Genera</i>	<i>Species</i>
Myxophyceae	9	11
Bacillariales	23	31
Chlorophyceae	17	15
Total	49	57
<i>Zooplankton</i>		
Protozoa	15	17
Rotifera	24	32
Crustacea	8	9
Total	47	58
Grand Total	96	115

Table 1 shows the relative proportion of constituent plankton groups, at various stations, to the total net plankton. This table is based upon data collected over a period of eighteen consecutive months and expresses the average percentage composition of each constituent group in relation to total net plankton at each station.

The significance of these data lies in the fact that all stations show a close similarity to each other in their average percentage composition of the major plankton groups. This indicates that plankton, introduced at Station 1 by the outlets of the two lakes, maintained its proportion of constituent groups for the 5 miles of river under investigation. The proportion was especially well maintained between total phytoplankton and zooplankton. This demon-

TABLE 1. Average Percentage Composition of Plankton.

Organisms	STATIONS			
	1	2	3	4
Phytoplankton				
Myxophyceae.....	10.00	11.20	15.17	17.36
Bacillariales.....	75.00	70.00	71.00	71.00
Chlorophyceae.....	2.00	6.65	4.21	.94
Total.....	87.00	87.85	90.38	89.30
Zooplankton				
Protozoa.....	11.00	10.75	8.26	9.23
Rotifera.....	1.50	1.17	1.19	1.25
Crustacea.....	.50	.23	.17	.22
Total.....	13.00	12.15	9.62	10.70
GRAND TOTAL.....	100.00	100.00	100.00	100.00

strates rather clearly that there were no significant sources of plankton supply other than the lakes. In the case of Myxophyceae and Chlorophyceae a rather noticeable variation does exist between stations. This variation is explained by additions of these groups from growths occurring at the margins of the river. However, the increase in percentage of these groups over that at Station 1 is rather insignificant and does not disturb the original proportion to any great extent.

Qualitatively, the Myxophyceae show a very irregular production and constitute from 1 to 25 per cent of the total net plankton. Bacillariales were always found to be the dominant group, constituting from 30 to 90 per cent of the total net plankton. Chlorophyceae never exceeded 12 per cent and often were absent. Protozoa showed the greatest irregularity among the zooplankton and constituted from 1 to 20 per cent of the total net plankton. This irregularity was due to seasonal variations of *Ceratium* and *Dinobryon* in the lakes. Rotifera and Crustacea showed seasonal variations but neither composed more than 5 per cent of the total net plankton at any time. Thus, even though the individual groups did vary within certain limits, the ratio between zooplankton and phytoplankton remained almost constant.

COMPARISON OF STATIONS

Table 2 represents data from plankton collections taken at each station on the river. These data demonstrate that at all times the lake plankton entering the river decreased as it progressed down stream. This phenomenon was demonstrated for total net plankton (Fig. 4) and for each of the following plankton groups: diatoms (Fig. 5), Rotifera (Fig. 6), and Crustacea (Fig. 7).

This quantitative decrease of lake plankton as it passed down stream was not limited to any one section of the river, but involved the entire 5

miles investigated. The factors responsible for the plankton decrease were effective shortly after plankton entered the river and continued as long as any plankton remained. It is a significant fact that plankton at any particular station always showed a greater quantity than at any station below it and a smaller quantity than at any station above it. However, the percentage of decrease between stations showed a variation at different times of the year but there was always a decrease of total net plankton of not less than 40 per cent between Stations 1 and 4. Station 2 showed a very consistent decrease which is of considerable significance since the distance involved was only 1 mile. On several occasions this decrease approached 50 per cent and on August 12, 1932 (Table 2), it was 83 per cent. However, the average decrease between Stations 1 and 2 for the 18 months was approximately 25 per cent.

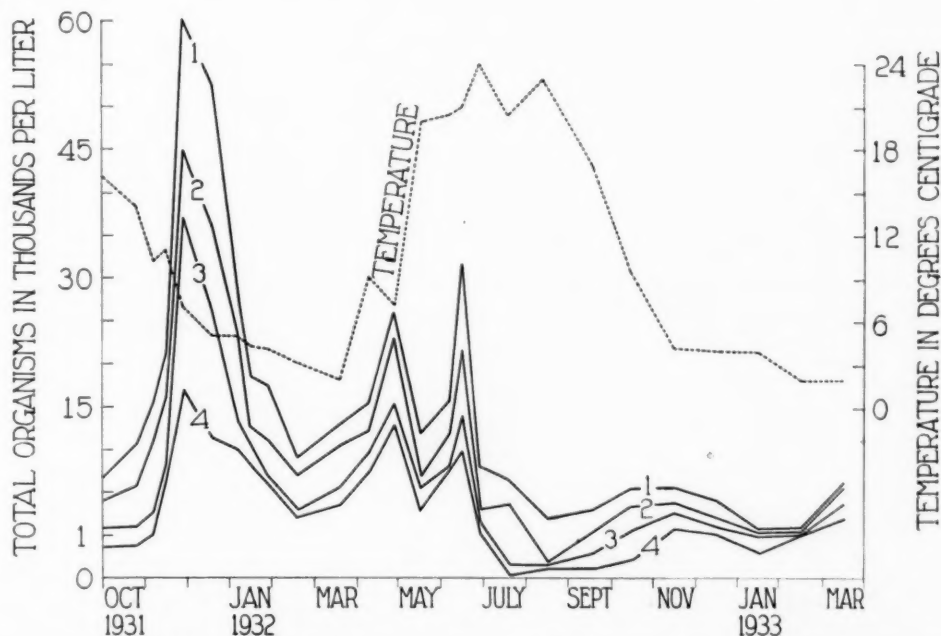


FIG. 4. Graphs showing total net plankton, in thousands per liter, at each station on the Huron River, from October, 1931, to March, 1933. Also a graph showing the temperature in degrees centigrade at Station 1 during the same period. Collecting stations indicated by Arabic numerals.

It is believed that the quantitative decrease of lake plankton entering the river is related to the following factors: amount of aquatic vegetation, water level, and volume of lake plankton entering the river. In July, 1932 (Table 2), there occurred a decrease of 99 per cent between Stations 1 and 4 while in February, 1933, there was a decrease of 41 per cent. Thus, at certain times of the year, lake plankton entering the Huron River disappeared almost completely by the time it had flowed the distance of 5 miles, while at other times, plankton decreased only 40 per cent over the same distance. This wide variation probably has its explanation in certain environmental factors which likewise exhibit a definite fluctuation during the year.

The influence that the above factors have on the decrease of lake plankton entering the river may be indicated by correlating the intensity of these factors with the per cent of plankton decrease at various times of the year. From October 21 to November 11, 1931 (Table 2), lake plankton entering the river underwent an average decrease of 91 per cent as it flowed from Station 1 to 4. During this time aquatic vegetation was abundant, water level was relatively low, and the average quantity of plankton organisms entering the river was 10,500 per liter. From November 18 to December 2, 1931, lake plankton entering the river underwent an average decrease of 77 per cent as it flowed from Station 1 to 4. At this time aquatic vegetation in the river was less abundant than during the preceding period, water level

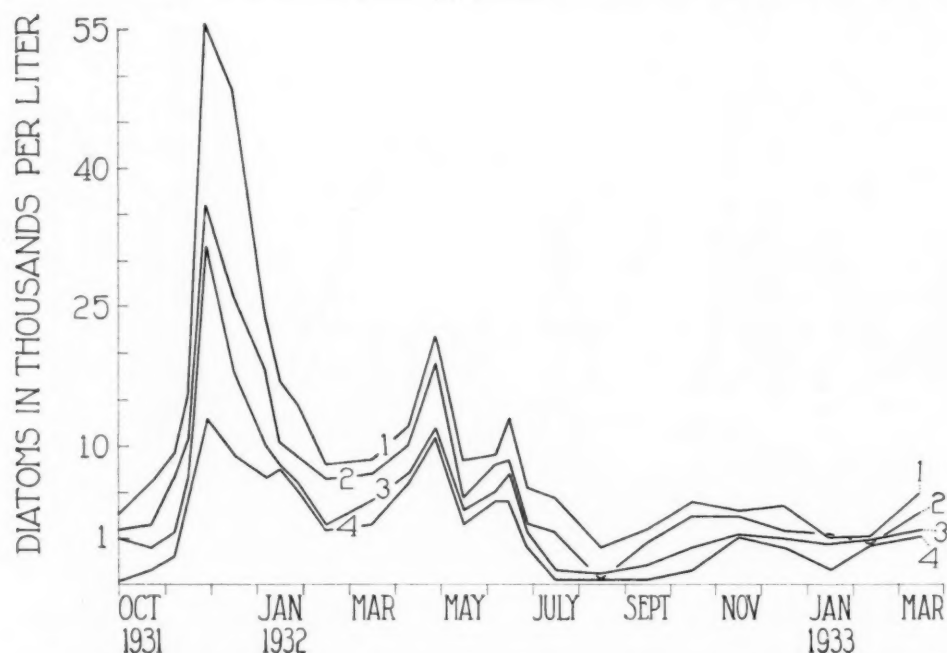


FIG. 5. Graphs showing total net diatoms, in thousands per liter, at each station on the Huron River, from October, 1931, to March, 1933. Collecting stations indicated by Arabic numerals.

was relatively high, and the average quantity of plankton organisms entering the river was 44,600 per liter. From January 6 to March 14, 1932, plankton entering the river underwent an average decrease of 66 per cent as it flowed from Station 1 to 4. In comparison to the preceding period, aquatic vegetation was scarce, water level was lower, and the average quantity of plankton organisms entering the river was 17,000 per liter. From April 20 to June 9, 1932, the average quantity of plankton organisms entering the river was 20,000 per liter, and the average decrease of this plankton as it flowed from Station 1 to 4 was 58 per cent. Aquatic vegetation in the river was scarce, and the water level was higher than the preceding period. From June 22 to October 18, 1932, the average quantity of lake plankton entering the

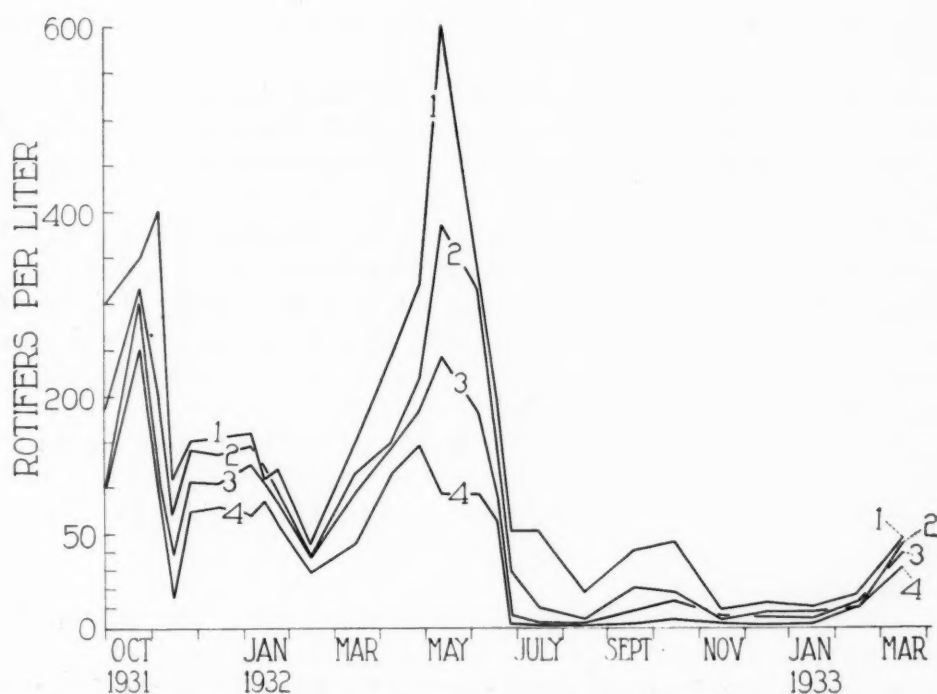


FIG. 6. Graphs showing the quantity of plankton rotifers per liter, at each station on the Huron River, from October, 1931, to March, 1933. Collecting stations indicated by Arabic numerals.

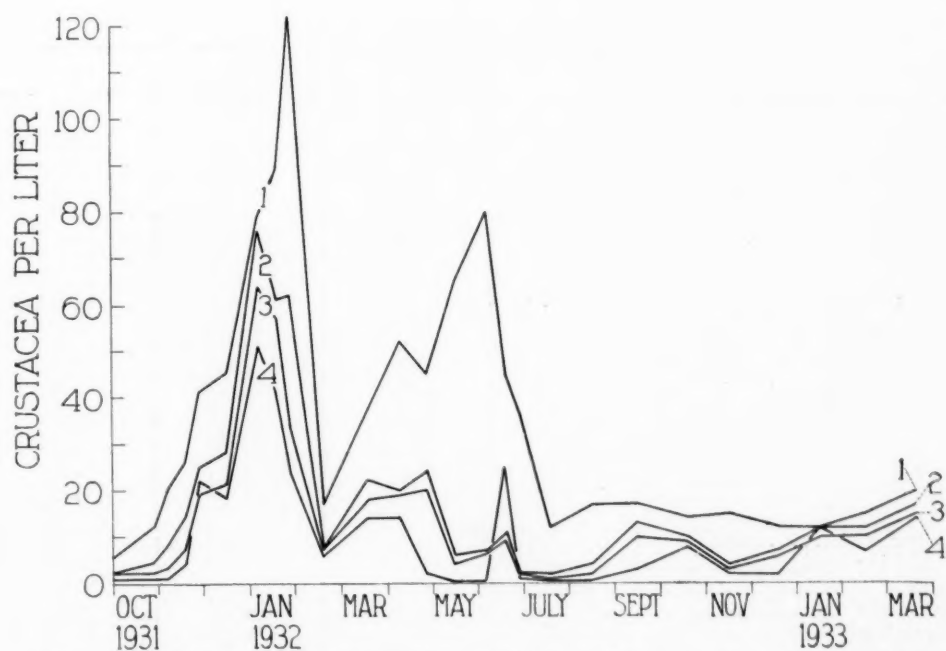


FIG. 7. Graphs showing the quantity of plankton Crustacea per liter, at each station on the Huron River, from October, 1931, to March, 1933. Collecting stations indicated by Arabic numerals.

river was 5,000 organisms per liter, and this plankton underwent an average decrease of 92 per cent as it flowed from Station 1 to 4. Aquatic vegetation in the river was abundant, and water level was lower than the preceding period. From November 30 to December 10, 1932, the average quantity of plankton organisms entering the river was 4,800 per liter, and this plankton underwent an average decrease of 73 per cent as it flowed from Station 1 to 4. Aquatic vegetation in the river was less than the preceding period, and water level was higher. From January 25 to March 20, 1933, the average quantity of plankton organisms entering the river was 3,000 per liter, and the average decrease of this plankton was 54 per cent as it flowed from Station 1 to 4. Aquatic vegetation in the river was scarce, and water level was lower than the preceding period.

It is evident from the above data that lake plankton flowing from Station 1 to 4 underwent the greatest decrease during times when aquatic vegetation was most abundant and water level the lowest. Also, the smallest decrease of this plankton, flowing from Station 1 to 4, was at times when aquatic vegetation in the river was scarce and water level was high. The intermediate degrees of decrease occurring between these extremes can be correlated with variation of environmental factors. It is believed that the importance of quantity of plankton entering the river lies in the fact that the greater the number of organisms per liter of water the greater the chance

TABLE 2. Total plankton organisms per liter in the Huron River, 1931, 1932, 1933.

Date		STATIONS			
		1	2	3	4
October	21.....	6,555	4,087	1,602	701
October	28.....	10,712	5,619	1,802	751
November	11.....	20,470	11,208	2,303	996
November	18.....	21,385	14,384	8,846	5,819
November	26.....	59,991	45,165	37,325	16,896
December	2.....	52,599	35,963	26,125	11,496
January	6.....	27,539	23,620	13,289	9,919
January	13.....	19,646	12,683	10,462	8,026
January	27.....	17,593	11,255	6,917	6,181
February	27.....	9,002	7,046	2,936	2,334
March	14.....	12,588	10,537	5,513	3,559
April	20.....	15,249	12,370	9,763	7,530
April	27.....	26,468	23,642	15,205	13,246
May	25.....	12,043	7,037	5,465	3,877
June	1.....	15,818	12,192	8,237	7,895
June	9.....	31,805	21,544	13,972	10,169
June	22.....	7,914	3,074	2,122	1,208
July	8.....	6,502	3,623	349	12
August	12.....	1,921	323	308	203
September	29.....	3,152	1,053	620	207
October	18.....	5,559	3,470	1,024	413
November	30.....	5,576	3,810	2,610	1,607
December	10.....	4,027	2,017	1,513	1,005
January	25.....	1,571	1,424	1,318	618
February	28.....	1,883	1,625	1,325	1,120
March	20.....	6,075	5,555	3,360	2,049

that they will be removed from the water as they flow down stream. This particular point is discussed in a later section of this paper dealing with Bessey Creek and Maple River.

BESSEY CREEK-LANCASTER LAKE SITUATION

CONSTITUENT PLANKTON ORGANISMS

During this study, 84 species and 91 genera of plankters were identified. The complete list of plankters and a general discussion of them will appear in another paper. These were distributed among the plankton groups as follows:

<i>Phytoplankton</i>	<i>Genera</i>	<i>Species</i>
Myxophyceae	10	11
Bacillariales	21	21
Chlorophyceae	16	12
Total	47	44
<i>Zooplankton</i>		
Protozoa	11	8
Rotifera	25	26
Crustacea	8	6
Total	44	40
Grand Total	91	84

The composition of plankton entering Bessey Creek from Lancaster Lake varied greatly during different summers and at different times of the same summer. Since this study was limited to summer months when a minimum quantity of plankton was present, it is impossible to determine anything significant by computing the average percentage composition as was done for the Huron River.

During August, 1932, zooplankton constituted quantitatively more than 50 per cent of the total net plankton of Bessey Creek; however, phytoplankton was present in significant amounts. Protozoa was the largest group and constituted approximately 50 per cent of the total net plankton. The predominant protozoans present at this time were *Ceratium* and *Dinobryon*. Rotifera and Crustacea appeared in quantities much greater in proportion to phytoplankton than was shown for the Huron River. Collections taken from Lancaster Lake during the summer of 1932, showed that the qualitative plankton composition of lake and stream was nearly identical.

Collections during early July, 1933, showed a predominance of phytoplankton over zooplankton in the stream. However, the latter was present in significant quantities. By July 17, 1933, net phytoplankton had completely disappeared so far as significant numbers were concerned. At this time, only an occasional algal form was encountered while making the routine quanti-

tative counts. Scarcity of phytoplankton continued until late August, 1933, when an increase of diatoms occurred. Collections in Lancaster Lake confirmed this scarcity of algal forms for the greater part of the summer of 1933. Collections in November, 1933, showed a large quantity of phytoplankton, especially the diatoms, and collections in early July, 1933, showed the presence of phytoplankton indicating that only during summer months does zooplankton predominate. Thus, a study of this situation makes it possible to determine if lake plankton predominated by zooplankton undergoes a quantitative decrease as it flows down stream.

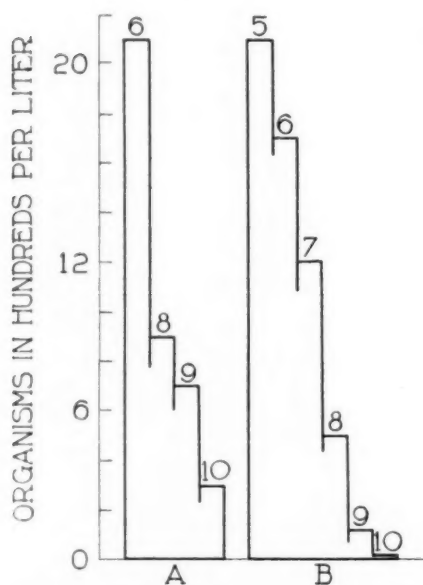


FIG. 8. A—Graph showing total net plankton, in hundreds per liter, at four stations on Bessey Creek, August 25, 1932. Collecting stations indicated by Arabic numerals.

B—Graph showing total net plankton, in hundreds per liter, at six stations on Bessey Creek, July 12, 1933. Collecting stations indicated by Arabic numerals.

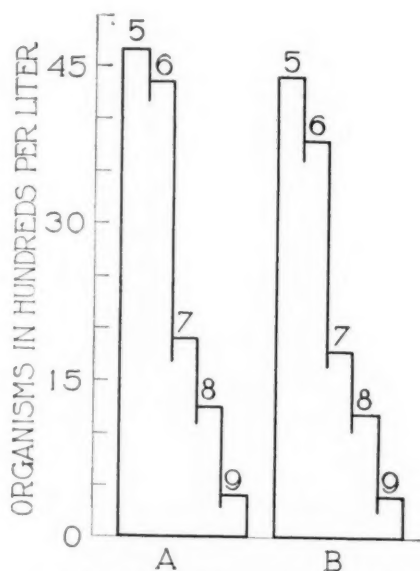


FIG. 9. Graphs showing quantity of plankton, in hundreds per liter, at five stations on Bessey Creek, November 4, 1933. A—Total net plankton; B—Total net plankton diatoms. Collecting stations indicated by Arabic numerals.

COMPARISON OF STATIONS

Entire Investigated Portion

The qualitative composition of total net plankton collected at each station on Bessey Creek was very similar to plankton leaving Lancaster Lake. When the qualitative plankton composition at a station differed from that of the outlet it was due to elimination of certain plankters from more distant stations or to addition of detached epiphytic forms. The quantity of plankton added by the stream itself was very insignificant and was not considered in this study.

Table 4 represents data from plankton collections taken at each station on Bessey Creek. These data show that lake plankton entering the stream always decreased in quantity as it flowed down stream. This phenomenon was demonstrated for the total net plankton (Fig. 8) and for each of the following plankton groups: diatoms (Fig. 9, B), Rotifera (Fig. 10, C), and Crustacea (Fig. 10, E).

This quantitative decrease of lake plankton as it flowed down stream was not confined to any special section of the stream but occurred throughout the entire investigated portion. Usually, the decrease of plankton was not uniform between stations, but at no time was the quantity at a station less than the quantity at a station below it or greater than at a station above it.

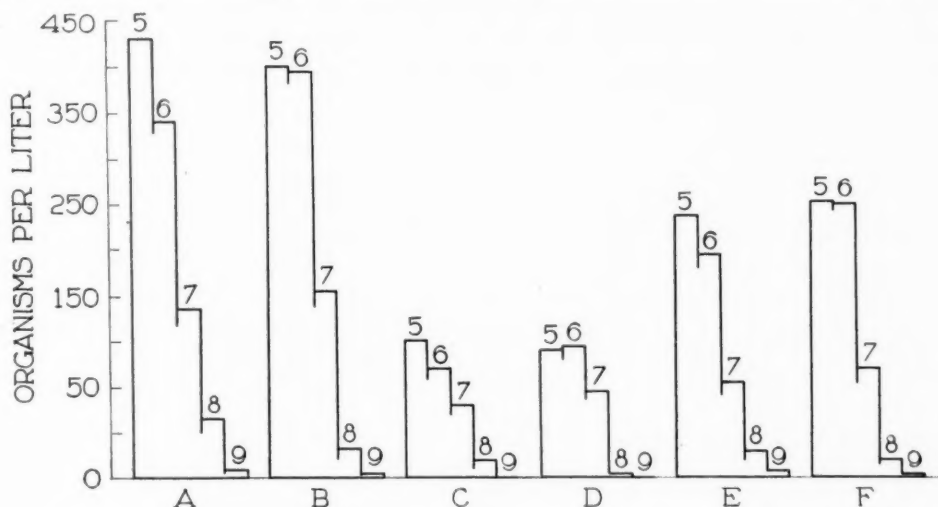


FIG. 10. Graphs showing quantity of plankton, per liter, at five stations on Bessey Creek, before and after vegetation removal, August 11, 1933, and August 14, 1933, respectively, between Stations 5 and 6. A—Total net plankton before vegetation removal; B—Total net plankton after vegetation removal; C—Total plankton rotifers before vegetation removal; D—Total plankton rotifers after vegetation removal; E—Total plankton Crustacea before vegetation removal; F—Total plankton Crustacea after vegetation removal. Collecting stations indicated by Arabic numerals.

The greatest decrease per unit of distance occurred within a short distance from the lake in a section of the stream that supported an abundance of vegetation. On August 25, 1932, a plankton collection (Fig. 8, A), which is representative of this particular summer, showed a decrease of 58 per cent between Stations 6 and 8, a distance of 0.2 mile. At Station 10 the quantity of plankton was only 14 per cent of that at Station 6. The collection of July 12, 1933 (Fig. 8, B), representative of this particular summer, likewise showed a pronounced decrease of lake plankton within a distance of 0.2 mile from the lake and nearly an absence of plankton at Station 10.

The quantitative decrease, effective for total net plankton entering the stream, was likewise effective for each individual plankton group. However, the Myxophyceae and Chlorophyceae, in several instances, showed an

increase in quantity due to additions from the margins of the stream. These additions were irregular and constituted a very small percentage of the total net plankton. The diatoms, composing approximately 50 per cent of the phytoplankton, always showed a decrease as they flowed down stream. At times when diatoms constitute a large percentage of the total net plankton they may be very important in producing the general features of a quantitative decrease between the lake and stations down stream (Fig. 9). Rotifera and Crustacea showed a decrease between stations nearly as consistently as did the diatoms. However, these two groups never occurred in large quantities but during summer they composed nearly the entire total net plankton. The quantity of these groups was always much greater at the outlet of Lancaster Lake than at any station on the stream. Almost invariably the most pronounced decrease of these groups occurred within 0.5 mile from the lake and often within a distance of a few meters.

Vegetation Zone

The fact that the greatest decrease of lake plankton entering the stream occurred in late summer in sections containing much vegetation suggested that vegetation was partly responsible for the decrease. In order to determine how vegetation might function in removal of plankton from the stream, a special study was made of the vegetated portion between Stations 5 and 6. In this study, numerous plankton collections were taken while vegetation existed under normal conditions. Later, vegetation was removed and more collections were taken.

Before Vegetation Removal

A quantitative plankton decrease occurred between Stations 5 and 6 (Table 4) throughout the summer of 1933. This decrease is of considerable significance when it is realized that the distance involved was only 15 meters. A conspicuous feature of this portion of Bessey Creek was the abundance of aquatic vegetation existing throughout the summer but increasing in abundance from early July to a maximum in late August. The vegetation consisted of a heavy mat of *Lyngbya* and the following macrophytes:

Potamogeton Richardsonii
Potamogeton natans
Potamogeton zosterifolius
Potamogeton Friesii
Najas flexilis
Utricularia vulgaris

Equisetum fluviatile
Myriophyllum sp.
Hippuris vulgaris
Nymphaea advena
Scirpus validis

A bed of aquatic vegetation of similar composition, except for *Lyngbya*, existed in Lancaster Lake near the outlet. However, there was a short distance between the vegetation bed of stream and lake containing little or no vegeta-

tion. *Lyngbya* at Station 5 formed what appeared to be a floating mat but actually it extended from surface to bottom of the stream and was held in position by intermingled growths of the macrophytes mentioned above. By August, 1933, this mat was so extensive that it nearly extended across the stream at Station 5 and down stream for a distance of about 8 meters. The remaining portion of the stream between Stations 5 and 6 was heavily vegetated but it lacked *Lyngbya*. Vegetation was so abundant in this zone that water leaving Lancaster Lake had to flow through some portion of the bed on its course down stream. Thus vegetation, especially that portion containing *Lyngbya*, acted more or less as a strainer for water leaving the lake. Throughout the summer of 1933 plankton leaving the lake underwent a quantitative decrease of 20 to 58 per cent as it flowed through this vegetation bed. The decrease was not due to the removal of any one plankton group or individual plankter but rather to the removal of some of each plankton component involved.

In order to determine how this vegetation was functioning in removal of plankton small quantities of vegetation, occurring between Stations 5 and 6, were collected and examined for adhering plankters. Examination of a small portion of the *Lyngbya* mat revealed the presence of many organisms normally occurring in plankton at Station 5, in addition to numerous non-plankters. The filaments were closely intermingled and matted, producing the characteristics of a very effective strainer. Large numbers of diatoms, the predominant species in the plankton, were identified in this mat especially at the time when they were most abundant in the lake. Large numbers of rotifers and Crustacea, the same species occurring in the plankton, were likewise observed in this mass of vegetation. In most instances these plankters were alive but often the remains of diatoms and hard parts of rotifers and Crustacea were observed. When algal forms dominated the plankton of Lancaster Lake, July 5-10, 1933, they appeared in greater numbers in the vegetation mat than did zooplankters. Later in the summer of 1933, when zooplankters were dominant, they appeared in greater numbers in the vegetation mat than did phytoplankters. Thus, it seemed that the *Lyngbya* mat was actually straining out plankton organisms leaving the lake. It was also observed that during the summer an accumulation of material formed around the stems of macrophytes. Rate of accumulation of this material increased throughout the summer. Examination showed this material to consist of particles of sediment, portions of decaying macrophytes, gelatinous stalks of ephytic diatoms, filamentous algae, numerous invertebrates not normally occurring in the plankton, and the predominant plankters represented in plankton at Station 5. This study involved no attempt to make a quantitative comparison between plankters found adhering to vegetation and those occurring in the plankton at Station 5. However, nearly every predominant plankter leaving the lake was represented in the *Lyngbya* mat or in the accumulations around stems of macrophytes.

After Vegetation Removal

On August 11, 1933, a plankton collection was taken at each station on Bessey Creek before any vegetation was removed. Immediately after this collection approximately all vegetation between Stations 5 and 6 was removed by means of a rake. On August 14, 1933, three days after vegetation removal, another collection was made at each station on the stream. Results of these two collections are compared in Figure 10 and in Table 3. To con-

TABLE 3. Organisms per liter in Bessey Creek before and after vegetation removal between Stations 5 and 6. Vegetation was not removed between Stations 6 and 7, 7 and 8, 8 and 9. Compare plankton numbers horizontally.

Vegetation	STATIONS				
	5	6	7	8	9
Before Removal.....	431	340	134	28	3
After Removal.....	401	398	151	16	2

firm these results a collection was made on November 4, 1933 (Table 4). This collection showed that lake plankton underwent a decrease as it flowed down stream but it was the least pronounced between Stations 5 and 6, as was true for August 14, 1933.

It is not possible, from this study, to state exactly how aquatic vegetation functions in removal of plankton from flowing water but it seems reasonable from the data herein presented that vegetation acts as a strainer. It is possible that organisms removed by this method accumulate in the meshes of the closely intermingled masses of vegetation or on stems of individual plants. It is also possible that some of these organisms remain alive for some time after their removal, others are doubtless eaten by non-plankton inhabitants

TABLE 4. Total plankton organisms per liter in Bessey Creek, 1932, 1933.

Date		STATIONS					
		5	6	7	8	9	10
August	22.....	4,159	1,313	704	...
August	23.....	4,064	1,031	708	...
August	25.....	2,174	914	704	302
August	26.....	2,712	615	510	...
July	5.....	3,251	2,025
July	10.....	2,117	1,149
July	12.....	2,092	1,732	1,196	484	103	3
July	17.....	508	244	217
July	21.....	661	441	16
July	26.....	168	100	15	4	...
July	31.....	383	221
August	9.....	259	119
August	11.....	431	340	134	32	3	...
August	14.....	401	398	151	16	2	...
August	18.....	1,845	1,942
November	4.....	4,651	4,347	1,902	1,258	431	...

of the vegetation mass, and others die, adding to the accumulation of sediment. The greater the accumulation of material the more effective is the straining action. It appears that as material increases around the stems of plants it is often torn loose in masses which settle to the bottom or float down stream until they attach to some object. Examination of sediment accumulated beneath vegetation beds showed that its composition was nearly identical with material adhering to plants, which confirms the belief that the accumulated materials settle to the bottom.

MAPLE RIVER-DOUGLAS LAKE SITUATION

CONSTITUENT PLANKTON ORGANISMS

During the investigation of Maple River, 108 plankters were identified. There were 102 genera but in several instances no species identification was attempted. This plankton list will appear in a separate paper. Plankters were distributed among the plankton groups as follows:

<i>Phytoplankton</i>	<i>Genera</i>	<i>Species</i>
Myxophyceae	16	17
Bacillariales	22	24
Chlorophyceae	17	16
Total	55	57
<i>Zooplankton</i>		
Protozoa	14	12
Rotifera	23	28
Crustacea	10	11
Total	47	51
Grand Total	102	108

Plankton entering Maple River from Douglas Lake showed a distinct predominance of phytoplankton over zooplankton, throughout the period of investigation. Bacillariales always occurred in larger numbers than any other plankton group and constituted on the average about 75 per cent of the total net plankton. At the outlet of Douglas Lake, the minimum number of diatoms at any one time was 1,000 per liter while the maximum was 40,900 per liter. Myxophyceae were always present at the outlet in numbers not less than 1,000 per liter and not more than 2,500 per liter. This group constituted not more than 10 per cent of the total net plankton. Chlorophyceae were always present but often in small numbers and constituted a small percentage of the total net plankton. Zooplankton seldom constituted more than 10 per cent of the total net plankton and often much less. The three zooplankton groups were consistently represented in each collection but always in smaller numbers than the phytoplankton groups. In general, the plankton composition of Maple River resembles that of the Huron River more closely than it does that of Bessey Creek.

COMPARISON OF STATIONS

Entire Investigated Portion

Total net plankton collected at each station on Maple River had a qualitative composition similar to the plankton leaving Douglas Lake. If there were a difference it was due to elimination of certain plankters from the more distant stations or to the addition of detached epiphytic forms. The number of organisms added by the stream was insignificant thus they received no consideration in this study.

Table 6 represents data from plankton collections taken at various stations on Maple River. These data show that plankton entering Maple River from Douglas Lake decreased quantitatively as it flowed down stream. The

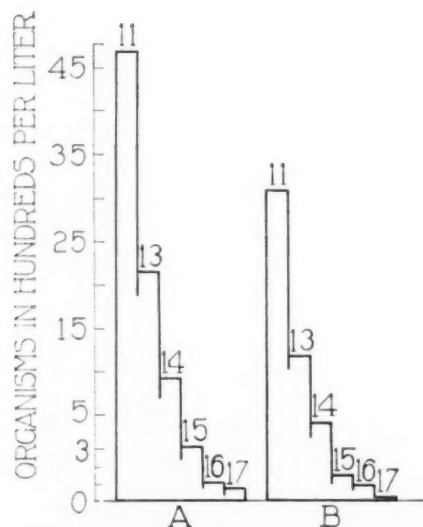


FIG. 11. Graphs showing quantity of plankton, in hundreds per liter, at six stations on Maple River, August 27, 1932. A—Total net plankton; B—Total net plankton diatoms. Collecting stations indicated by Arabic numerals.

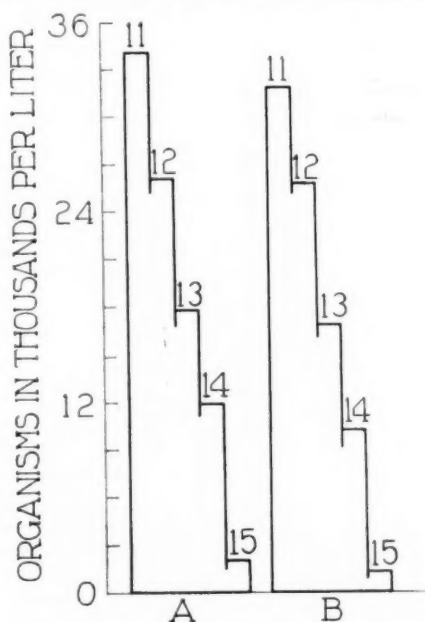


FIG. 12. Graphs showing quantity of plankton, in thousands per liter, at five stations on Maple River, October 28, 1932. A—Total net plankton; B—Total net plankton diatoms. Collecting stations indicated by Arabic numerals.

general features of this decrease are nearly identical with those exhibited by Bessey Creek and Huron River. Usually the greatest decrease per unit of distance took place a short distance from the lake in a heavily vegetated part of the stream. However, this decrease was not limited to any one section of the stream but involved the entire portion investigated. This phenomenon was demonstrated for total net plankton (Fig. 12, A) and for each of the following plankton groups: diatoms (Fig. 12, B), Crustacea (Fig. 13, A), and Rotifera (Fig. 13, B). When Chlorophyceae and Myxophyceae were present in significant numbers they likewise exhibited this quantitative decrease.

Vegetation Zone

A special study was made on the section of Maple River between Stations 11 and 13 for the purpose of determining if vegetation was an important factor in explaining the decrease of lake plankton after entering the stream. This section of the stream was characterized by an abundance of vegetation confined to definite beds. During early summer, vegetation occurred in small quantities and the stream showed a high water level. In late summer, vegetation reached a maximum production and the water level was very low. Thus, in this section of the stream the proportion of vegeta-

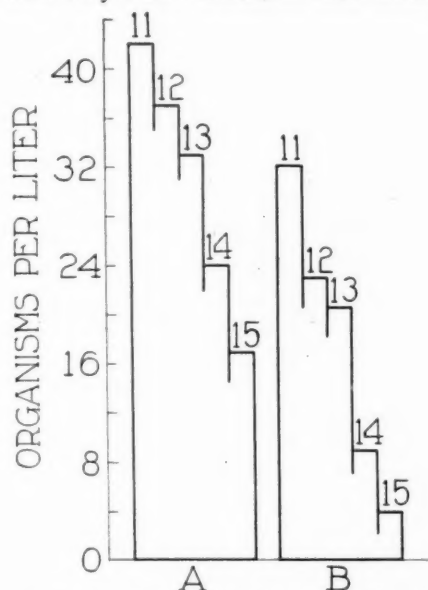


FIG. 13. Graphs showing quantity of plankton, per liter, at five stations on Maple River, October 28, 1932. A—Total plankton Crustacea; B—Total plankton rotifers. Collecting stations indicated by Arabic numerals.

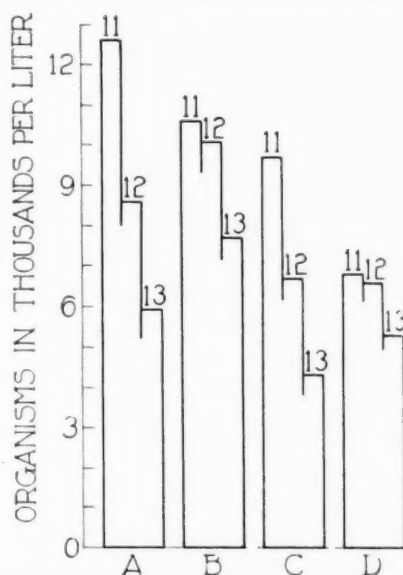


FIG. 14. Graphs showing quantity of plankton, in thousands per liter, at three stations on Maple River, August 28, 1933, before and after vegetation removal between Stations 11 and 12. A—Total net plankton before vegetation removal; B—Total net plankton after vegetation removal; C—Total net plankton diatoms before vegetation removal; D—Total net plankton diatoms after vegetation removal. Collecting stations indicated by Arabic numerals.

tion to volume of water increased from early to late summer, a factor believed to be of considerable significance in relation to this problem. Aquatic plants composing the greater percentage of the vegetation were:

Chara sp.

Najas flexilis

Potamogeton natans

Potamogeton heterophyllus

Elodea canadensis

Scirpus validis

Before Vegetation Removal

Each collection (Table 6) showed that plankton leaving the lake underwent a significant quantitative decrease as it flowed from Station 11 to 13.

The collection of August 27, 1932 (Fig. 11), showed a decrease of approximately 54 per cent between these stations, involving a distance of 20 meters. At this time, the volume of water leaving the lake was small and was confined to a heavily vegetated channel, between Stations 11 and 13, not more than 2 meters wide. On October 27, 1932, the plankton underwent a 70 per cent decrease as it flowed from Station 11 to 13. This collection was taken during the autumn overturn of Douglas Lake, thus a larger quantity of plankton was entering the stream. However, the water level and abundance of vegetation in the stream was about the same as during the August collection. The following summer, 1933, when this study was resumed the water level was high and vegetation was present in small quantities. Thus the proportion of vegetation to volume of water was very much smaller than during the October collection of 1932. Collections from June to early August of this summer showed that plankton flowing from Station 11 to 13 underwent a decrease of not more than 20 per cent. But in late August when the water level was again low and vegetation abundant there occurred a decrease of 50 per cent or more between these two stations.

Results obtained from this study of vegetation between Stations 11 and 13 revealed many conditions which were similar to those found in vegetation beds of Bessey Creek. Small quantities of vegetation were examined microscopically for adhering organisms and it was observed that the predominant organisms of the plankton were present in large numbers, in addition to numerous non-plankters. Plankters were found in the accumulations around stems of individual plants. The general nature of this material was similar to that described for Bessey Creek. Likewise, sediment beneath the vegetation, on examination, revealed large numbers of living and dead plankters associated with masses of amorphous material. It was evident that many plankters were removed from water as it flowed through the vegetation bed and these became associated with accumulations on stems of plants or settled to the bottom along with sediment and various kinds of débris.

Study of this vegetation between Stations 11 and 13 from early to late summer made it possible to secure certain information concerning formation of material around stems of plants and its relation to the decrease of lake plankton as it flowed through this portion of the stream. In late June, the small amount of vegetation occurring in this zone contained little or no adhering material and at this time there occurred a small decrease of plankton as it flowed from Station 11 to 13. Later in the summer accumulations on the stems of plants became very pronounced and likewise a large quantitative plankton decrease occurred in this zone. Careful examination of plant stems in early summer showed a complete absence of adhering material in some instances and in others stems showed the presence of certain filamentous algae, epiphytic diatoms with branched gelatinous stalks and masses of what appeared to be in part bacteria. Certain of these plants were marked, making it possible to examine the same plant periodically through-

out the summer. It was found that as the accumulations increased various kinds of non-plankters such as, insect larvae, turbellarians, stalked protozoans and various epiphytic algae, became more abundant. In general, this type of material which formed on submerged stems and leaves of plants was partly responsible for the removal of organisms from the plankton. It seemed that the greater the accumulation the more effective it became as a strainer. In late summer, accumulations were so great that portions of them became detached and either floated down stream or sank to the bottom. On several

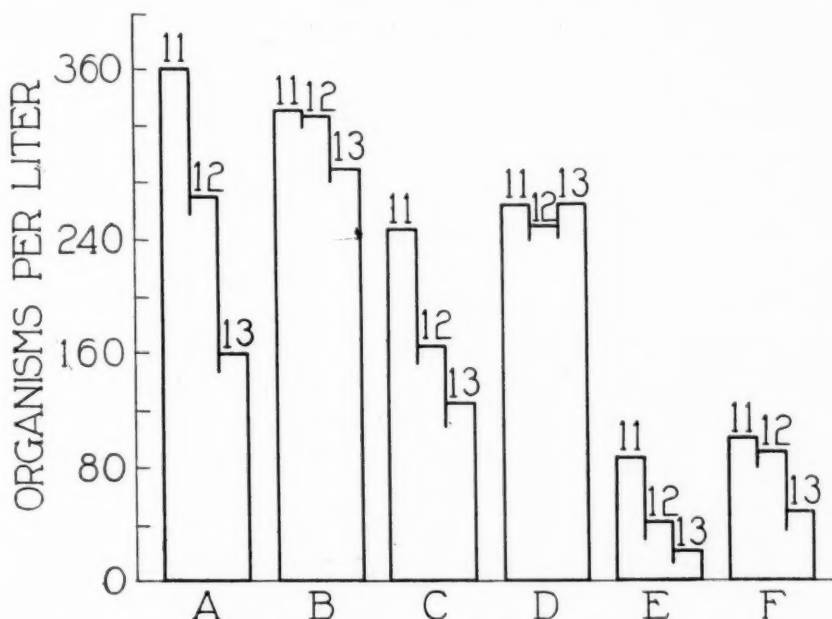


FIG. 15. Graphs showing quantity of plankton, per liter, at three stations on Maple River, August 28, 1933, before and after vegetation removal between Stations 11 and 12. A—Total plankton Protozoa before vegetation removal; B—Total plankton Protozoa after vegetation removal; C—Total plankton Crustacea before vegetation removal; D—Total plankton Crustacea after vegetation removal; E—Total plankton rotifers before vegetation removal; F—Total plankton rotifers after vegetation removal. Collecting stations indicated by Arabic numerals.

occasions, this vegetation zone was disturbed by walking through it resulting in the detachment of adhering material and sediment being thrown into suspension. Immediately following this disturbance, a collection taken at Station 13 invariably showed a quantity of plankton many times greater than one taken under normal conditions.

After Vegetation Removal

Data thus far presented indicate that vegetation is definitely related to the quantitative decrease of lake plankton as it flows down stream. It was realized that vegetation is not the only factor responsible for this decrease but, if it is as important as indicated, its removal would produce very evident results. Therefore, vegetation was actually removed between Stations

11 and 12 during its maximum growth in August, 1933, and the plankton study continued.

On August 28, 1933, a plankton collection was taken at Stations 11, 12, and 13 at 10:00 A.M. before any vegetation was removed. Immediately after this collection, vegetation was raked from the stream between Stations 11 and 12 until practically all plants were removed. However, vegetation was left undisturbed between Stations 12 and 13. Another plankton collection was made at each of the three stations at 5:30 P.M. of the same day after the stream had sufficient time to clear. Results of these two collections are compared in Figures 14 and 15 and in Table 5.

TABLE 5. Organisms per liter in Maple River before and after vegetation removal between Stations 11 and 12. Vegetation was not removed between Stations 12 and 13. Compare numbers horizontally.

Vegetation	STATIONS		
	11	12	13
Before Removal	12,696	8,578	5,808
After Removal	10,496	10,270	7,493

The importance of vegetation as a factor in explaining the decrease of lake plankton as it flows down stream is clearly demonstrated by data in Table 5. Before vegetation was removed plankton leaving the lake underwent a 32 per cent decrease as it flowed from Station 11 to 12, and approximately the same decrease as it flowed from Station 12 to 13. This is rather representative of other collections during late summer in this section of the stream. After vegetation was removed, between Stations 11 and 12 but not between Stations 12 and 13, lake plankton flowing from Station 11 to 12 underwent practically no decrease, but decreased 27 per cent between Stations 12 and 13. The influence that this vegetation had on the various plankton groups is illustrated in Figures 14 and 15. Further analysis of data from this study showed that each predominant plankter was effected by the vegetation and all to approximately the same degree. Thus, when lake plankton decreases quantitatively on flowing through a vegetation bed it is not due to the removal of any one plankton group or individual plankter, but rather to the removal of some of each predominant form.

On November 4, 1933, two months after vegetation had been removed between Stations 11 and 12, a collection was taken (Table 6) to confirm the previous findings. At this time, lake plankton flowing from Station 11 to 12 underwent practically no decrease but decreased 20 per cent between Stations 12 and 13.

Non-Vegetation Zones

The most pronounced quantitative decrease of lake plankton as it flowed down stream almost invariably occurred in vegetated sections. However,

certain non-vegetated sections exhibited a small decrease throughout the summer and often it became rather conspicuous during autumn. That portion of Maple River between Stations 13 and 15 was studied for the purpose of determining what factors other than vegetation might aid in producing the observed plankton decrease. This part of the stream was characterized by shallow water free from vegetation except on the margins. On August 27, 1932, lake plankton flowing from Station 13 to 15 underwent a decrease of 87 per cent. On October 28, 1932, there occurred an 88 per cent decrease between the same stations. These collections were made at a time when this section of the stream was dammed in several places with large accumulations of leaves, fragments of dead vegetation and fallen branches from near-by trees. An examination of this material revealed the presence of large numbers of the predominant plankters occurring at Station 11. Diatoms were the most numerous but nearly every predominant plankter occurring at the outlet was represented in this material. Most of the leaves and branches were coated with a slimy sediment containing various epiphytic algal forms, and it was to this material that plankters seemed to adhere. Most of these were loosely attached and could easily be removed by moving the leaves back and forth in the water. Many plankters adhering to this material were living but remains of many others were observed. The collection of July 8, 1933, showed that lake plankton flowing from Station 13 to 15 underwent a decrease of only 38 per cent. This was taken at a time when this section of the stream contained little débris such as leaves and fallen branches. The decrease of plankton flowing from Station 13 to 15 while very pronounced is not as great per unit of distance as that occurring between Stations 11 and 13. The distance from Station 11 to 13 is only 20 meters and from Station 13 to 15 is 0.3 mile.

Lake plankton flowing down stream often underwent a small but consistent quantitative decrease in sections of the stream where there was an absence of vegetation and obstructing débris. A conspicuous feature of such sections was deposits of dark flocculent sediment on the margins. This deposition extended from the outer margin of the water to approximately 0.5 meter towards mid-channel but the outer limits showed the thickest deposition. Examination of this material revealed the presence of certain organisms normally occurring in the plankton, especially the following predominant diatoms: *Asterionella formosa*, *Fragilaria crotonensis*, and *Melosira varians*. Considerable numbers of *Ceratium hirundinella*, *Keratella cochlearis*, *Polysarthra trigla*, small numbers of nauplii and *Cyclops* sp. were present. Each of these plankters occurred regularly in the plankton at the outlet and together constituted a large percentage of the total net plankton.

In an attempt to account for these plankters in sediment, small pans were used to collect sediment at various positions across the stream. When the contents of these pans were centrifuged and examined microscopically they revealed the presence of numerous plankters. Material deposited in

the pans resembled in many respects the composition of sediment on the margins of the stream. Those pans nearest the margins contained the largest deposition of material while those in mid-channel contained the smallest. There was no attempt to make a quantitative comparison between organisms of the sediment and the plankton but qualitatively there was a striking resemblance. A feature common to sediments deposited on the stream margins and in the pans was that almost invariably the contained plankters had small particles of débris attached to them and in many instances several plankters were attached together by a mass of débris. Most plankters were dead but some living individuals were observed.

Sediment pans were distributed across the stream in the vegetation bed between Stations 11 and 13, and considerable material was deposited in them. This material was nearly identical in composition to that adhering to stems of plants and resembled that deposited on the margins of the stream in non-vegetated sections.

These observations on Maple River suggest that some plankters were removed from the water by sedimentation. It was not definitely demonstrated, however, that this process was an important factor in producing a conspicuous quantitative decrease of the plankton flowing down stream, but it is believed that it does function to a certain extent in quieter water and probably to a large extent in vegetation beds. Most data supporting this belief were derived from examination of numerous collections of sediment and bottom ooze from vegetation beds, pools, and margins of shallow water. The qualitative composition of this material was very similar in all instances and showed the presence of large numbers of organisms normally occurring in the plankton.

TABLE 6. Total plankton organisms per liter in Maple River, 1932, 1933.

Date		STATIONS					
		11	12	13	14	15	17
August	22.....	93
August	24.....	8,172	52
August	26.....	63
August	27.....	4,721	2,169	931	284	75
October	27.....	24,051	16,417	7,138	1,311
October	28.....	34,081	26,264	17,759	11,936	2,121
June	26.....	3,026	2,486	1,881
June	28.....	5,617	4,114
July	8.....	4,721	3,881	2,877	2,393
August	4.....	3,017	1,945	1,722	412
August	17.....	5,331	4,328	3,077
August	28.....	12,696	8,578	5,808
August	28.....	10,496	10,270	7,493
November	4.....	42,300	40,500	32,300	16,700	12,100

PHYSICAL-CHEMICAL DATA

There was no attempt to make an extensive physical-chemical study of lakes and streams involved in this investigation. Analyses were made for the purpose of determining the general physical-chemical nature of lakes and to discover if there were significant chemical changes in water as it left them and flowed through those sections of streams exhibiting a pronounced plankton decrease.

A considerable amount of physical-chemical data from Douglas Lake has been published (Welch, 1928; Welch and Eggleton, 1932, 1935; Eggleton, 1931); therefore further analyses were unnecessary. Also, unpublished data secured by Professor Paul S. Welch for a chemical study of water flowing from Douglas Lake into Maple River made further chemical determinations unnecessary in the stream. These data showed that there was no significant chemical change in water as it flowed from Douglas Lake to a distance of 30 meters or more down Maple River. Determinations for hydrogen-ion concentration, dissolved oxygen, free carbon dioxide, carbonates, bicarbonates, and temperature were made at frequent intervals from a position in the lake approximately 10 meters from the outlet to a distance of 30 meters down Maple River. A similar study was made on the Bessey Creek-Lancaster Lake and Huron River situations with similar results.

DISCUSSION

Several authors have stated that plankton in certain portions of streams shows a quantitative decrease as it passes down stream. Richardson (1921) observed a 62 per cent decrease within a distance of 120 miles on the Illinois River. Galtsoff (1924) reported a quantitative decrease of approximately 45 per cent within a distance of 60 miles in a certain portion of the Mississippi River. Forbes (1928) stated that the quantity of plankton in the middle region of the Illinois River was nearly 15 times greater than the quantity in the region of the mouth. Also, Eddy (1932) found a quantitative difference in plankton of the upper and lower portions of the Sangamon River. Thus, it is evident from these and other reports, that a quantitative plankton decrease in streams had been observed previous to this investigation. However, none of the previous investigations had been on a stream without tributaries or pollution and deriving its water directly from a lake. Up to the present time, plankton investigations on streams have dealt with a plankton produced by the stream itself or the combined plankton of several streams and often one or more lakes. These situations contain many complex problems not only in respect to plankton composition but also physical and chemical conditions as well. Likewise, previous investigations have not been confined to an intensive study of a restricted portion of a stream but rather to a general survey of the entire river or some large portion of it. In most instances, previous investigators have

only suggested an explanation for the observed quantitative plankton decrease in streams, except in heavily polluted waters. In several instances, the quantitative decrease has been attributed to current but no one has conclusively shown this to be an important factor in itself. The present investigation has been an attempt to determine the nature of a plankton decrease in restricted sections of streams and of certain factors that are definitely related to it. This has been made possible by choosing situation deriving their water and included plankton from typical lakes, therefore eliminating many complicating factors in respect to plankton composition and physical-chemical conditions. It is realized that these data demonstrate the nature of a quantitative decrease of only typical lake plankton when entering a stream, but it is believed that the factors responsible for this decrease are also possible factors causing the decrease of other plankton in streams.

A study of the Huron River, Maple River and Bessey Creek showed that lake plankton entering a stream undergoes a quantitative decrease as it passes down stream. This decrease was demonstrated irrespective of season and was effective not only for total net plankton and various plankton groups but for the predominant individual plankters as well. The quantitative decrease in these streams is not uniform but small or large in different portions depending upon the presence or absence of certain environmental factors. It was shown that the quantitative decrease was definitely related to aquatic vegetation, to various kinds of *débris* and possibly to sedimentation. Other factors are associated with a quantitative plankton decrease but most of them are less conspicuous in their effects than those mentioned above.

Aquatic vegetation is believed to be one of the most important factors causing a quantitative plankton decrease in the streams investigated. A study of the Huron River for 18 consecutive months, demonstrated that the periods of greatest decrease occurred at times when the quantity of aquatic vegetation was the largest. Bessey Creek and Maple River, studied during two summers, showed that lake plankton underwent a small decrease as it flowed down stream in early summer when vegetation was scarce and a pronounced decrease in late summer when vegetation was abundant. Likewise, portions of these streams showing the greatest plankton decrease per unit of distance were those supporting a heavy growth of vegetation. The section of Bessey Creek between Stations 5 and 6, a distance of 15 meters, exhibited a decrease of 20 to 58 per cent when vegetation was most abundant. A vegetation bed of Maple River between Stations 11 and 13, a distance of 20 meters, showed a plankton decrease of 50 to 70 per cent at times of maximum vegetation production. The portions of these streams containing little or no vegetation throughout the summer likewise exhibited a consistently low plankton decrease. An intensive study of vegetation zones showing a very high percentage of decrease per unit of distance re-

vealed the fact that when vegetation was removed there no longer existed the pronounced plankton decrease.

It is rather evident that vegetation is related to the quantitative decrease but it is less evident how it functions. It can readily be seen how a dense mass of vegetation like the *Lyngbya* mat, between Stations 5 and 6 on Bessey Creek, could actually strain out plankters from water passing through it but how individual macrophytes remove plankton seems more difficult to understand. A large number of microscopical examinations of submerged stems and leaves of aquatic vegetation showed the presence of numerous epiphytic algae, filamentous algae, bacteria, stalked Protozoa, rotifers with organs of attachment, Turbellaria, insect larvae and large quantities of sediment in addition to many organisms normally occurring in the plankton. It was thus observed that this accumulation of material on macrophytes increased greatly from early to late summer. In early summer, individual plants supported such a small quantity of adhering material that it could be detected only by microscopical examination. By late summer, the accumulation of material was present in quantities that were easily visible and often so great that detached masses were seen floating down stream. Microscopical examination of plants in early summer showed the presence of only a few epiphytic algae, especially certain branched gelatinous stalked diatoms, filamentous algae, bacteria and a few adhering plankters. As the summer progressed, these non-plankton forms increased in number as well as the plankters. An attempt was made to determine if the rate of accumulation of material varied among different species of macrophytes but since it was nearly impossible to employ quantitative methods for this comparison definite conclusions are lacking. However, it appeared that *Najas flexilis* and *Chara* sp. accumulated material more rapidly than other plants. An explanation for this might lie in the fact that both plants have leaves with spine-like projections offering better conditions for straining out material from water. However, the composition of adhering material appeared to be nearly identical for all plants examined.

These observations suggest that aquatic plants are not effective plankton removers in early summer since they contain little adhering material. As the summer progresses, epiphytic forms which almost invariably attach themselves at right angles to their substratum, increase in number and probably strain out many other organisms from water. In many instances, these epiphytic forms had adhering to them filamentous algae, such as *Spirogyra* sp., *Mougeotia* sp., *Fragilaria crotensis*, and *Melosira varians* which were so closely intermingled that a very effective straining device was produced. When such a combination was present on many plants composing a vegetation bed a large quantitative plankton decrease occurred within a very short distance, and many predominant plankters were found in this mass. If large numbers of plankters were being removed by this method, as it seemed certain they were, the question naturally arises as to

their ultimate fate. Plankters would not continue to accumulate on plants indefinitely without forming conspicuous masses. However, large accumulations were observed but when they reached a certain size portions became detached and either floated down stream, becoming attached to other objects, or sank immediately to the bottom. Without doubt many of these plankters were consumed by other inhabitants of the accumulated material.

Débris, such as decaying vegetation, accumulations of twigs and branches from trees, and especially dead leaves are believed to be definitely related to the quantitative plankton decrease which occurred in Maple River during the autumn of 1932. That portion of Maple River between Stations 13 and 15 contained little or no vegetation throughout the entire investigation and likewise it showed a small quantitative plankton decrease except in late summer and early autumn when this section was partially clogged with dead leaves and other débris. At this time, a quantitative plankton decrease of approximately 87 per cent occurred within a distance of 0.3 mile, showing a distinct contrast to the average summer decrease. Microscopical examination of leaves and débris forming the dams showed the presence of certain epiphytic algae, a slimy sediment and large numbers of predominant plankters. The plankters were not firmly attached but could be rather easily removed by shaking the leaves in water. Many plankters were alive but remains of dead individuals were also rather numerous. Among and beneath leaves composing the dams were large accumulations of sediment which, on examination, showed a composition almost identical with material adhering to leaves. These observations indicate that when plankters came in contact with exposed surfaces of leaves and other débris they either became attached and later dropped to the bottom or possibly were carried to the bottom immediately by settling material. This suggests that objects occurring in streams collect plankters on their exposed surfaces.

It has been shown that sedimentation was a possible factor in producing a quantitative plankton decrease in certain sections of Maple River. Sediment near the margins of the stream and that deposited in experimental collecting pans distributed across the stream contained many organisms normally occurring in plankton. A large deposition of sediment occurred on the margins of the stream where current was slowest but deposition was small in mid-channel where current was swiftest. It is believed that settling of plankton in Maple River is hastened by the large quantity of suspended particles of marl invariably present in the region of the lake outlet. Numerous observations have shown that these particles of marl and plankters often become associated and, under such conditions, it is reasonable to believe that these plankters settle rather quickly. Examination of sediment and bottom ooze in various portions of Maple River indicated that considerable quantities of plankton were settling out, especially in quiet waters near the margins, in pools, and to a great extent in vegetation beds. If sedimentation is an important factor in producing a quantitative

plankton decrease in Maple River, it is believed to vary considerably with rate of current and amount of suspended material in water. These results partially confirm those of Richardson (1921) who observed a rather large plankton decrease in a portion of the Illinois River. He stated, "These losses were greatest when the current was the slowest and settling consequently easiest." Also, he stated, "The river plankton is constantly settling to the bottom to an important degree as is shown by the composition of the bottom ooze and stomach contents of small invertebrates living in and on it."

Water level is probably related to a plankton decrease in streams. A rise in water level as shown by the Huron River almost invariably results in a smaller plankton decrease provided other conditions remained approximately the same. This was especially true during the spring and fall rains. Probably the significance of this lies in the proportion of water volume to exposed surfaces to which plankton might adhere. An increase in water volume results in the inundation of new areas above the old water line and deepens water of the main channel. In most instances, new objects are encountered by water over the inundated areas but probably very few of them have a surface favorable for plankton adherence, since they do not possess accumulations of sediment and epiphytic algae. Likewise, a deepening of water in the main channel reduces the proportion of water coming in contact with submerged objects. This suggests that a rise in water level results in a smaller proportion of plankton coming in contact with surfaces to which they might adhere, thus resulting in a smaller plankton decrease. A low water level was almost invariably accompanied by a large plankton decrease. This suggests that during periods of low water the proportion of water volume to exposed surfaces is smaller, thus more plankton come in contact with exposed surfaces.

Schroeder (1897), from an investigation on the Oder, concluded that the volume of plankton present in any stream is inversely proportional to rate of current. Kofoid (1903, 1908) states that the most important relation of current to plankton is its effect in determining the length of time in which plankton can breed. Allen (1920) came to the conclusion that water currents above a moderate speed are distinctly inimical to plankton development. Likewise, Van Oye (1926) and Galtsoff (1924) found current to be related to a scarcity of plankton in certain portions of streams. The current of the Huron River, Maple River and Bessey Creek is relatively slow and it was not shown to be definitely related to the quantitative plankton decrease except possibly in case of sedimentation which occurred more rapidly in quieter waters.

The quantitative plankton decrease occurring in streams investigated was not related to pollution, dilution, change in temperature or chemical change. Temperature did not vary more than 2°C. throughout the investigated courses of streams, and dilution by tributaries and pollution were absent in all situations. It was shown that there was no significant chemi-

cal change in water as it left lakes and flowed through those sections of streams exhibiting a pronounced plankton decrease.

It is evident that the quantitative plankton decrease exhibited by streams investigated is not caused by any one factor but by several (aquatic vegetation, débris, sedimentation, and others). One factor may be more important in one section of a stream than in another but the total plankton decrease occurring between the outlet of a lake and the most distant station on the stream may be due to the combined effect of several factors. The greatest plankton decrease per unit of distance occurred in those sections of streams possessing more than one effective factor. It seems that the greatest plankton decrease in streams is produced by collection of plankters on surfaces of objects with which they come in contact. Volume of water in proportion to amount of exposed surfaces in a stream is much less than in a lake; therefore, lake plankton entering a stream has a greater chance of coming in contact with exposed surfaces to which it might adhere.

SUMMARY

1. A qualitative-quantitative plankton study designed to determine the fate of typical lake plankton in streams was made on portions of the Huron River, Maple River and Bessey Creek, Michigan. Each portion studied derived its water from a typical lake and was without pollution or tributaries.
2. An eighteen months study of that portion of the Huron River formed by the outlets of Portage and Base Line Lakes demonstrates that lake plankton entering this portion of the river undergoes a quantitative decrease as it flows down stream, irrespective of season.
3. Summer studies on Maple River and Bessey Creek demonstrate that plankton entering from Douglas Lake and Lancaster Lake respectively undergoes a progressive, quantitative decrease as it passes down stream.
4. Quantitative plankton decrease in each of these streams is exhibited (a) by total net plankton; (b) by each large plankton group; and (c) by certain predominant individual plankters.
5. Plankton decrease was not uniform in all parts of each stream but varied with the presence or absence of certain environmental factors.
6. The greatest plankton decrease per unit of distance invariably occurred in heavily vegetated sections of each stream. A decrease of approximately 70 per cent occurred within a distance of 20 meters in a heavily vegetated portion of Maple River and a 60 per cent decrease within a distance of 15 meters in a vegetated zone in Bessey Creek. When the vegetation was removed from these sections, plankton decrease was no longer conspicuous.
7. Vegetation may act as a strainer in removing plankton from flowing water. Likewise, plankters may adhere to accumulated material on submerged stems and leaves of macrophytes.

8. Various kinds of submerged débris and objects may possess surfaces favorable for plankton accumulation.

9. Proportion of water volume to exposed surfaces of submerged objects probably influences the chance of plankters coming in contact with surfaces favorable for plankton accumulation.

10. Plankters settling to the bottom, either alone or in association with inanimate material, may aid in producing a plankton decrease.

11. Temperature, pollution, dilution from tributaries, current and a change in chemical conditions are not factors causing a plankton decrease in the streams investigated.

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ECOLOGY OF MIXED PRAIRIE IN WEST
CENTRAL KANSAS

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ECOLOGY OF MIXED PRAIRIE IN WEST CENTRAL KANSAS*

INTRODUCTION

The mixed prairie was first recognized as a distinct plant association by Clements (1920) who described its nature and range and the groupings of the dominants. Its relationships to true prairie and short-grass plains are further discussed by Weaver and Clements (1929). The association in Kansas occupies a broad belt across the western half of the state but gives way to true prairie near a central north-south line. Despite its importance and vast extent but few studies of an ecological character have been made in typical mixed prairie.

Bruner (1931) described the southward extension of mixed prairie through Oklahoma and its relation to true prairie and short-grass plains. Shantz (1911) gave an excellent discussion of the short-grass plains of eastern Colorado, especially that portion lying west of Kansas. The natural vegetation eastward from the Rocky Mountains to the 98th meridian from Canada to Texas has also been described by Shantz (1923). Pool (1914) studied the sandhills of Nebraska, and Sarvis (1920, 1923) reported on the mixed prairie of central North Dakota. Numerous papers by Clements (1916, 1934, and 1936) elucidate many of the problems of the grasslands.

Rather numerous publications on the true prairie are of much value in showing its relationships to the mixed prairie. The most comprehensive is that by Weaver and Fitzpatrick (1934). Aldous (1934) studied the eastern Kansas prairies in relation to burning; Schaffner (1913, 1926) has made extensive studies in central and eastern Kansas; and Weaver and Himmel (1931) reported on the environment of the prairie during a long period of years. Extensive studies on water content and root development of prairie plants have been made throughout several of the grassland associations (Weaver, 1919, 1920).

A comprehensive comparison of the environmental factors and growth of grassland vegetation in true prairie, mixed prairie, and short-grass plains was made by Weaver (1924) and Clements and Weaver (1924). The mixed prairie station, selected after extensive reconnaissance as centrally located, was maintained at Phillipsburg, Kansas, 70 miles due north of the area of the present research. The three years during which water content of soil, temperature, humidity, and evaporation were measured were, fortunately, years of average rainfall and indicate clearly the intermediate nature of the mixed prairie among grassland climates. Differences in vegetation and response to extreme drought in true and mixed prairie have been described recently by Weaver and Albertson (1936).

* Contribution from the Department of Botany, University of Nebraska, No. 105.

The present research is concerned with the detailed structure of several types of mixed-prairie grassland, the reasons for their distribution, the interrelations of the plants both above and below ground, and measurement of the intensity of the edaphic and aerial environmental factors.

LOCATION, EXTENT, AND HISTORY OF THE AREA

The area selected for study comprises approximately 750 acres of mixed prairie located in Ellis County in west central Kansas about 2.5 miles west of the city of Hays. This prairie is a portion of the Fort Hays Military Reservation which was established in 1865 and abandoned in 1889. In 1900 the Federal Government, through an act of Congress, gave the land included in the reservation to the state of Kansas to be used as a state experiment station, a state park, and a state college. The legislature of the state of Kansas accepted this grant and the Fort Hays Kansas State College came into possession of 4,000 acres, including the area of special study. This land was fenced and has been lightly pastured by cattle and horses during the major portion of the time since its acquisition in 1900.

TOPOGRAPHY AND DRAINAGE

The rolling topography is typical of much of the prairie land of this section of the state. The altitude varies from slightly more than 2,000 feet in the lowlands to approximately 2,200 feet on the highest hills and tablelands (Fig. 1). A large winding ravine runs diagonally across the prairie.



FIG. 1. General view of the rolling topography of the mixed prairie near Hays, Kansas. The density of the vegetation varies with depth of soil to the underlying limestone which is here exposed on the south-facing slope.

Tributaries from many directions enter this ravine, causing a broken topography. A rather irregular, broad strip of nearly level tableland stretches between the heads of these tributary ravines and slopes rather gently to the brows of the hills where the descent is commonly abrupt to the fairly level land below.

Runoff water resulting from torrential rains is rapidly carried away by this system of drainage to a small stream running through the adjacent lowlands. During periods of excessive rainfall, however, shallow ponds of short duration are sometimes formed in the center of the ravines where basins have resulted from erosion.

GEOLOGY

The underlying rock is the Fort Hays limestone which is here exposed along its eastern edge (Fig. 2). It is the lower member of the Niobrara



FIG. 2. A typical view of the Fort Hays limestone near a hilltop. The blanket of soil and partially disintegrated rock on this northeast slope has been removed.

formation of the Cretaceous system. These layers of limestone cap the hills, being buried 2 to 9 feet deep by a mantle of residual soil. The rock is exposed only in outcrops on the brows and upper slopes of the hills. These deposits consist of a series of strata of soft, chalky limestone and shale, the layers varying in thickness from a few inches to several feet and having a total depth of approximately 55 feet (Bass, 1926).

SOILS

The fine-textured, silty, clay loam soils are a part of the western residual soil region of Kansas (Throckmorton, 1932). Those on the nearly level highlands and hillsides have been derived directly from the Fort Hays limestone but infiltrated with sand from overlying Tertiary deposits which have now been completely eroded. Soils on the lower hillsides and ravines have been gradually built up from eroded materials carried down the hills by water and gravity. Near the base of the hills, where the eroding processes have cut through the Fort Hays limestone, narrow strips or belts of soil are commonly found that have been derived from the upper portion of the Carlile shale.

On the rounded hilltops and tablelands the soils overlying the limestone are usually sufficiently deep to permit the unobstructed penetration of deeply rooted plants. The valley soils are also deep and fertile and only those of the upper slopes and limestone outcrops are thin and rocky.

GENERAL PLANT-LIFE CONDITIONS

The climate of this semiarid region is characterized by a moderately long growing season with only occasional rains, high temperatures, low relative humidities, and a relatively high wind velocity. There are occasional periods, often of several days duration, when desiccating hot winds promote great loss of water from both soil and vegetation. The average frost-free period extends from April 29 to October 13. Thus the growing season includes approximately 165 days.

The winters are usually mild, although temperatures of -10°F. or lower may occur over periods of several days. The precipitation is light. Snow has little value in replenishing soil moisture of uplands and exposed situations since most of it is swept by the wind into protected places.

The average annual precipitation at Hays for the 68-year period (1868 to 1935) is 22.84 inches. That for the growing season (April to September, inclusive) is 17.52 inches (Table 1). Yearly precipitation is subject to great variation. The 6-year period, from 1927 to 1932 inclusive, had an average annual precipitation of 27.76 inches or nearly 5 inches above the 68-year average. Moreover, that of the summer months was 21.52 inches. This 6-year wet period was followed by three years of unusual drought when the average annual precipitation was only 15.46 inches. This was 7.38 inches below the 68-year average and 12.30 inches less than the average for the 6 preceding years. It was during these latter three years that the present study was made.

Temperature and humidity are fully as variable as precipitation. In fact, the three are very closely related. When summer rainfall is insufficient to supply the demands of the growing vegetation, the air becomes dry and the temperature of soil and air immediately rise. During periods of

drought the average daily maximum air temperature is often between 95° and 110°F. The nights, however, are relatively cool. Relative humidity often decreases to 15 to 25 per cent during periods of extremely high temperatures. The wind is prevailing from the south. The average daily velocity by months during the growing season is 5 to 13 miles per hour. Average velocities for individual days, however, sometimes reach 25 to 28 miles per hour. Wind has a marked effect upon increasing evaporation. The saturation deficit is increased and transpiration is greatly increased. The south and southwest winds often assume the form of dust storms in spring and summer. The air may become so filled with dust that the sun is scarcely visible. Following the great drought of 1934, accumulated dust locally covered many areas of vegetation.

TABLE 1. Average monthly precipitation in inches for the years 1868 to 1935, 1927 to 1932, and 1933 to 1935, at Hays, Kansas.

Period	January	February	March	April	May	June	July	August	September	October	November	December	Average	
													Six summer months	Year
1868-1935....	.48	.81	.99	2.26	3.26	3.48	3.18	3.01	2.33	1.47	.84	.73	17.52	22.84
1927-1932....	.40	.73	1.35	2.34	2.86	6.11	3.47	3.91	2.51	2.25	1.66	.17	21.52	27.76
1933-1935....	.12	.56	.31	.91	3.11	3.21	.79	1.56	2.32	.56	1.21	.80	11.90	15.46

GENERAL VEGETATIONAL DISTRIBUTION

Three general types of vegetation with varying degrees of intermixtures are common in the area selected for study. The short-grass (*Bulbilio-Bouteloua*) type, constituting 30 per cent of the prairie, is found widely distributed over the nearly level uplands. Smaller areas and strips also occur at the bases of the hills, especially on south-facing slopes, where the soil is underlaid with an impervious clay. The most extensive type is that characterized by the little bluestem (*Andropogon scoparius*). It comprises 60 per cent of the area, occupying the hillsides and extending across shallow ravines. It also extends over the brows of the hills and far beyond where the slopes continue, but gives way more or less abruptly to short grasses on the level uplands (Figs. 3 and 4). The big-bluestem (*A. furcatus*) type is much more limited in extent, constituting about 10 per cent of the prairie. It occupies the deeper ravines, lower portions of gentle slopes, and well watered lowlands (Fig. 5).

The short-grass type is characterized by a predominance of buffalo grass and blue grama grass in about equal abundance, and by bunches of wire grass (*Aristida purpurea*) and little bluestem. The bunch grasses may occur as widely scattered plants, but increase in numbers with a more favorable



FIG. 3. General view of a portion of the area studied. The *Andropogon scoparius* consociation, which covers the slopes and occurs on the limestone outcrops, gives way on the level uplands (foreground and upper left) to the *Bulbilis-Bouteloua* type or faciation.



FIG. 4. Looking across a shallow ravine at *Andropogon scoparius* (dark) clothing the shallow soil and the short grasses (*Bulbilis-Bouteloua*, light) carpeting the upland in the distance. The enclosure (No. 1) is on the ecotone between the two communities.

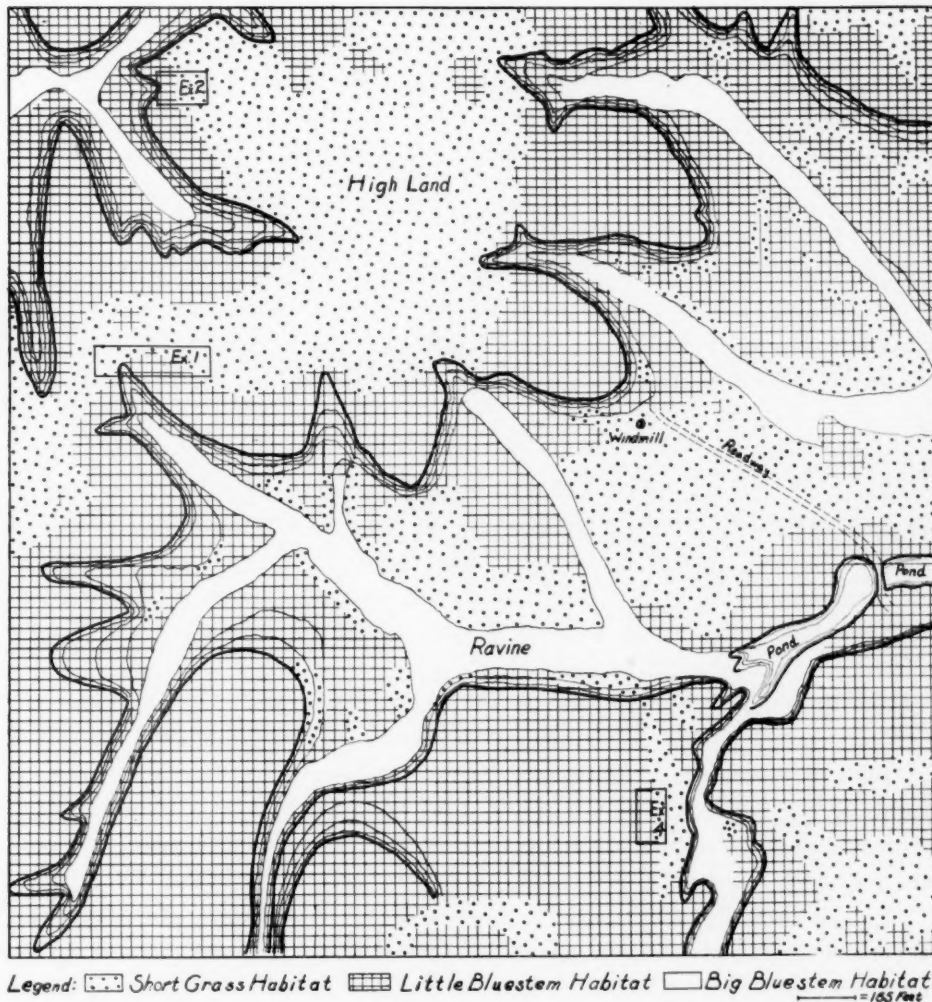


FIG. 5. Selected area of 160 acres showing the distribution of the 3 types of vegetation in relation to the topography. The heavy lines mark the brows of the hills. The broad belt of short grass near the roadway and windmill is the result of trampling. The locations of three experimental enclosures are shown.

water supply. *Sitanion clymoides*, *Bouteloua curtipendula* and *Agropyron smithii* are common species of much less importance.

Numerous grasses besides the dominant are found regularly in the little-bluestem areas. *Andropogon furcatus*, *Panicum virgatum* and *Bouteloua curtipendula* extend far up the hillsides. They are more or less replaced in drier situations near the brows of the hills by *Sporobolus pilosus*, *Bouteloua hirsuta* and *B. gracilis*.

Distribution of the little-bluestem type is largely controlled by the shallow depth of soil above the underlying limestone. On the nearly level uplands where a mature soil profile has developed, it is replaced by the short-grass type.

On the lowlands, where deep alluvial soil is moistened by run-in water, little bluestem is replaced by the taller grasses. Chief associates of the big bluestem are *Bouteloua curtipendula*, *Agropyron smithii* and *Sporobolus drummondii*, with smaller amounts of *Panicum virgatum*, *Elymus virginicus*, *E. canadensis*, *Sorghastrum nutans* and *Carex graxida*.

SOIL PROFILES

The three major types of vegetation occur on soils with distinctly different profiles. The soil profile exerts such a profound effect upon the water, air, and nutrient relations of the soil and, consequently, upon root extent and distribution that it warrants careful study.

TYPICAL UPLAND PROFILE

The soil layer on the highland varies in thickness from approximately 2 to 9 feet. The profile is generally more mature than that on either the hill-sides or lowland. A typical profile representative of the soils of the highlands is shown in Figure 6. It consists of the three horizons characteristic of mature soils in the "Black Belt" (Marbut, 1923) or Chernozem (Kellogg, 1936).

Horizon A, the zone of extraction, extends from the soil surface to a depth of approximately 20 inches. This zone is so designated because of the fact that certain soil constituents, especially calcium and magnesium carbonates and part of the colloidal clay, have been leached or eluviated. Freezing and thawing, wetting and drying, and the granulating effect of the fine plant roots on the soil have resulted in a very definite granular structure.

The silt and clay content of this fine-textured soil is high (36 and 30 per cent, respectively) as is also the hygroscopic coefficient, 12.4 per cent. Consequently the moisture equivalent and maximum water capacity are also high (Table 2).

There are three sub-horizons. Horizon A_1 extends from the surface to a depth of 8 inches. It is granular in structure and is brownish-black in color. Horizon A_2 is approximately 4 inches thick and lies immediately below horizon A_1 . It is slightly lighter in color and somewhat less granular than the upper layer. When exposed, it develops a network of small cracks running in many directions and forming irregularly shaped discs or plates varying in diameter from 0.5 to 2 inches. Horizon A_3 has a thickness of approximately 8 inches, and forms the lower layer of the zone of extraction. It appears to be a transition layer to the zone of concentration. It is brownish in color and is slightly columnar in places but slightly granular in others.

Horizon B, the zone of concentration, lies beneath the zone of extraction. It extends to a depth of approximately 38 inches. It is so designated because of the fact that many of the constituents removed from the zone of extraction are deposited in this zone. These accumulations, especially of colloidal

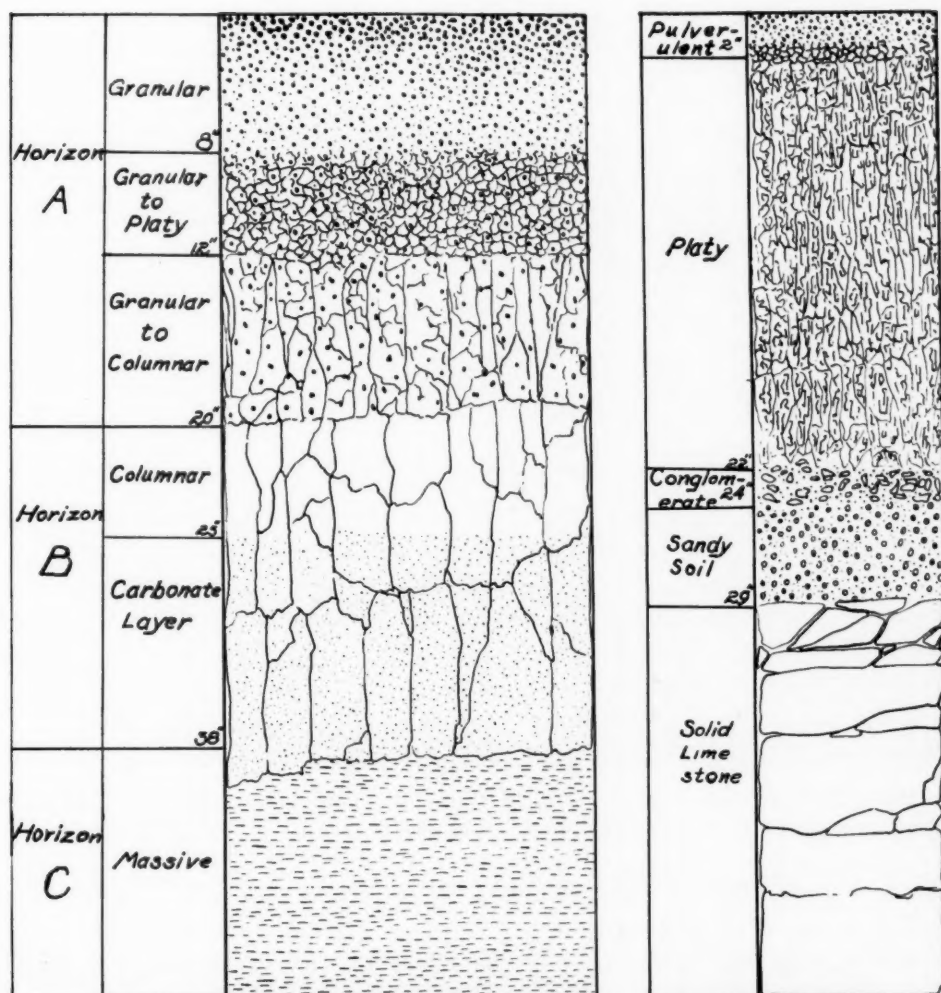


FIG. 6. (A) Typical mature profile of upland soil characterized by short-grass vegetation; (B) profile in shallow depression where vegetation is sparse.

clay, cause swelling and shrinking of the soil with an increase or decrease in water content and result in perpendicular lines of cleavage and the columnar structure characteristic of this horizon.

At 30 inches depth both silt and clay average about 35 per cent. The hygroscopic coefficient is 12.6 per cent and the maximum water capacity is 14 per cent greater than in the A horizon.

There are two rather distinct sub-horizons. Horizon B₁, a layer about 5 inches in thickness, is light brown in color, distinctly columnar, and contains a relatively small amount of calcium carbonate. Horizon B₂, 13 inches thick, lies between depths of 25 and 38 inches. It is yellowish-brown in color, distinctly columnar and is infiltrated with a major portion of the calcium carbonate accumulation. Here the columns are, in general, perpendicular. They vary in length from 6 to 12 inches and in diameter from 3 to 6 inches. The

TABLE 2. Soil texture and water relations of various soils at different depths.

Location	Depth, inches	Total sand, per cent	Silt, per cent	Clay, per cent	Hygro- scopic coef- ficient	Moisture equiva- lent	Maximum water capacity, per cent
Short grass.....	12	34.1	36.2	29.7	12.4	29.1	59.3
Short grass.....	30	28.2	34.8	35.0	12.6	29.6	73.4
Short grass.....	48	26.0	38.4	35.6	13.3	30.3	67.9
Depressions in short grass.....	12	28.5	29.3	42.2	15.6	32.4	66.6
Clay pockets in little bluestem..	60	32.4	10.5	57.1	20.5	53.2	103.0

calcium carbonate, through gradual accumulation, forms distinct whitish layers in the crevices between the columns and in other openings in the soil.

Horizon C, the massive zone, is that portion of the soil profile where neither extraction nor concentration has taken place. It lies immediately below horizon B and extends downward to approximately 9 feet to the limestone rock. The soil is yellowish in color, massive in structure, and fairly friable. Roots penetrate it easily.

This layer contains somewhat less total sand and proportionately more silt and clay than the horizon above. The hygroscopic coefficient (13.3) and moisture equivalent are also somewhat greater.

MINOR UPLAND PROFILE

The nearly level uplands commonly slope gently toward the brows of the hills. Since the underlying limestone layers are in an approximately horizontal position, it is obvious that the soil becomes progressively shallower from the highest levels downward toward the brows of the hills. On these gentle slopes where the soil is comparatively shallow, there are many small areas depressed 3 to 5 inches below the general level. The vegetation surrounding these shallow depressions is typical of that of the highlands, but that in the depressions is sparse, usually dwarfed, and much more shallowly rooted (Fig. 7).

The profile in the depressions is very different from that of the surrounding soil (Fig. 6). There is an upper layer, 2 to 4 inches in thickness, which is dark gray in color and pulverulent to granular in structure. The fine-textured, nearly impermeable layer lying immediately beneath varies in thickness from 12 to 20 inches. It is black in color, plastic when wet, and badly cracked when dry. Some of the cracks are perpendicular, forming distinct columns; others run in various directions forming a platy condition. The shrinking and cracking during drought is due to the very high content of clay, 42 per cent. Silt constitutes about 29 per cent of the soil and various



FIG. 7. Typical view of short-grass vegetation on a nearly flat hilltop. In the foreground is the edge of a shallow depression with its sparse vegetation.

sands (mostly fine) make up the remaining 29 per cent. The hygroscopic coefficient is 15.6 per cent. Beneath this black plastic layer is one of conglomerate about 3 inches thick. Below the conglomerate layer and above the solid limestone there lies a 6-inch layer of sandy clay. Water often covers the soil in these depressions for several days after a heavy rain.

PROFILE OF HILLSIDES

Due to the eroding effect of gravity, wind and water, the soils on the brows and sides of the hills vary considerably. In many places the badly disintegrated limestone is exposed at the surface between the scattered bunches of grass. In others, where the slope is more gentle, there has been a gradual accumulation of soil above the rock until a layer varying in depth from a few inches to approximately two feet has been formed. This layer is similar to the zone of extraction of the mature profile in many respects. The soil is dark gray to black in color and granular in structure. There are, however, many small pieces of limestone scattered throughout. Near the surface these rock fragments are scarce and not larger than one-half inch in diameter. In the deeper soil, however, they become progressively larger and more abundant until ultimately solid rock occurs.

In many places the layers of rock have perpendicular crevices varying in diameter from 1 to 15 inches. These crevices are filled with a sandy clay that has a relatively high maximum water capacity, representative samples averaging 103 per cent. The clay increment is 57 per cent, silt about 11, and total sand 32. The hygroscopic coefficient is very high, 20.5 per cent (Table 2). The rock deposits vary greatly in thickness; those near the top of the hills are often 10 to 12 feet thick and consist of several layers. Farther down the hillside, however, they may not exceed 2 feet in depth. Below this series of layers of relatively hard limestone, there is one consisting of much softer material.

Near the base of the hills there is a layer of soft shale several feet thick from which is derived a bluish clay soil highly impervious to water. Although this kind of soil occurs but intermittently as narrow belts along the lower slopes, it is always characterized by short grass. The profile in these relatively narrow strips of soil is somewhat more mature than that farther up the hillside. The zone of extraction forms a layer approximately 20 inches

deep. It is dark gray in color, granular in structure, and contains a fairly heavy mixture of limestone fragments usually not more than one-half inch in diameter. Lying immediately beneath this layer is one approximately 10 inches thick. It is gray in color, somewhat columnar, fine-textured and with comparatively few limestone pebbles. A third layer of soil is found at a depth of 30 inches. It is made up primarily of a blue clay.

PROFILE OF LOWLANDS

The profile of the lowland soil is not fully matured due to the fact that new soil is being constantly added. The upper 30 inches has in general, however, the characteristics of the zone of extraction of a typical mature profile (Fig. 8). It is granular in structure and black in color at the surface but gradually becomes lighter with

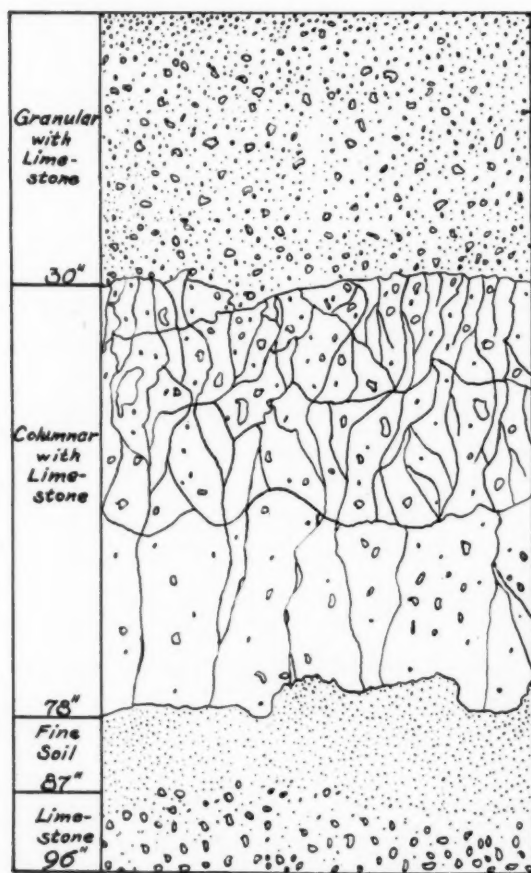


FIG. 8. Immature soil profile characteristic of lowland soil that supports a growth of big blue-stem.

depth. There are many limestone fragments, some one-half inch in diameter, scattered throughout this layer.

The zone of concentration is 48 inches thick. It is brown in color, only slightly columnar, and contains fragments of limestone which are scattered throughout as in the layer above. The carbonate layer is lightly concentrated throughout the zone.

Below the zone of concentration are alternate layers of brown soil and finely broken limestone pebbles. These layers occur in the position normally occupied by the massive layer in the mature profile.

RUNOFF

The distribution of vegetation indicates that the available soil moisture is increasingly greater from the highest to the lowest land. This is further borne out by moisture determinations made at various depths during the three years of study. This increase in water content is due in a large measure to runoff water.

Interceptometers were employed to determine the amount of runoff in different habitats. These consisted of boxes made of No. 22 galvanized iron, 3 feet long, 12 inches wide, and 24 inches deep. The boxes were well braced inside and furnished with a hinged, sloping roof, open 0.5 inch in front.

After selecting the station for installment, an excavation slightly larger than the interceptometer was made at right angles to the slope. The front side of the interceptometer was then fitted tightly against this wall with the upper edge about 0.25 inch below the soil surface. Soil was then tamped firmly about the box to hold it in place. The front edge was tightly sealed with soft asphalt to prevent erosion and loss of runoff water at the entrance to the interceptometer (Weaver and Noll, 1935). An area 3 feet wide, 33.3 feet long and parallel with the slope was enclosed by one-inch boards 4 inches in width. These were placed on edge in the soil to a depth of 3 inches and held firmly by nailing them to stakes driven into the soil. The accumulated water was removed and measured after each rain. The amount of runoff water was then calculated in terms of percentage of the rainfall.

Runoff water was measured from a short-grass area having a slope of 5.5 per cent, and another of little bluestem with a slope of 7.3 per cent. A standard rain gauge was operated near the runoff areas. For convenience, the runoff from showers of 0.5 inch or less is presented separately from that of heavier rains (Table 3).

All but one of the 15 showers recorded resulted in some runoff. The amount in the short-grass type averaged 1.4 per cent and varied from 1.0 to 2.2 per cent in 1934. The intense heat and drought of 1934 destroyed much of the vegetation causing the basal cover to be materially reduced. The runoff in 1935 was consequently increased. The amount averaged 2.4 per cent and varied from 1.0 to 4.4.

The runoff from the little-bluestem area, where the slope was 1.8 per cent

greater, averaged only 1.2 and ranged from 0.6 to 2.0 per cent in 1934. In 1935 the average runoff was 3.0 per cent.

The runoff from rains greater than 0.5 inch are shown in Table 4. It is significant that the percentage of runoff usually varied directly with the amount of rainfall. It is also greatly influenced by the manner in which the rain fell. Gentle rains, even though fairly heavy, resulted in relatively little runoff. Conversely, runoff from the torrential type was usually great.

The amount of runoff averaged 2.2 per cent and varied from 2.0 to 2.4 per cent in the short-grass type in 1934. The average in the little-bluestem area for the same period was only 1.7 per cent.

In 1935 the average runoff was 16 per cent with a range between 3.0 and 47.6. This is materially greater than that of the little-bluestem type where the variation was small and the average only 5.5 per cent.

An area of 200 square feet adjacent to the preceding was also enclosed. The upper half was clothed with short grasses and the lower one with little bluestem. A single interceptometer was placed at the lower end of the enclosure. Thus the runoff water from the short grass flowed onto the tract of little bluestem. Even with this extra supply of water from the short grass, percolation was sufficiently rapid in the bluestem soil to cause no material increase in the percentage of runoff. The amount in 1934, when the rainfall was less than 0.5 inch, averaged 1.4 per cent and ranged between 0.6 and 1.9 per cent. That in 1935 averaged 2.96 and varied from 1.96 to 3.9 per cent.

TABLE 3. Percentage of runoff from short grass (slope 5.5 per cent) and little bluestem (slope 7.3 per cent) and from bluestem when short-grass runoff entered the bluestem area, from rains less than 0.5 inch.

Date		Rainfall in inches	Short grass	Little bluestem	Short grass and little bluestem
June	29, 1934	0.17	1.02	0.55	1.12
July	5, 1934	.15	1.20	.85	1.14
August	1, 1934	.09	.00	.24	.62
August	13, 1934	.45	1.20	1.04	1.16
August	22, 1934	.22	2.02	1.83	1.82
August	23, 1934	.10	1.95	1.52	1.88
September	2, 1934	.26	2.17	2.09	1.72
Average		1.36	1.16	1.35
May	14, 1935	.22	3.03	2.64	2.80
May	22, 1935	.17	2.51	3.79	3.88
May	27, 1935	.27	3.10	3.60	3.76
June	5, 1935	.15	1.02	2.50	2.78
June	11, 1935	.50	2.03	3.01	3.16
June	26, 1935	.30	4.41	3.81	3.18
August	24, 1935	.20	1.52	1.68	1.96
August	28, 1935	.30	1.67	2.20	2.18
Average		2.41	2.90	2.96

TABLE 4. Percentage of runoff from short grass (slope 5.5 per cent) and little bluestem (slope 7.3 per cent) and from bluestem when short-grass runoff entered the bluestem area, from rains in excess of 0.5 inch.

Date		Rainfall in inches	Short grass	Little bluestem	Short grass and little bluestem
June	22, 1934	0.57	2.23	1.34	1.62
July	10, 1934	.52	2.02	1.71	1.86
August	30, 1934	.75	2.41	1.86	2.12
August	31, 1934	.60	2.30	2.19	2.26
October	18, 1934	.52	2.04	1.19	.58
Average		2.20	1.66	1.69
May	11, 1935	.75	2.64	2.02	2.50
May	13, 1935	1.85	20.98	4.12	5.20
June	1, 1935	1.60	47.60	14.50	25.20
June	16, 1935	1.37	23.55	6.24	11.52
June	25, 1935	.60	11.40	5.10	4.08
June	29, 1935	.60	21.90	6.84	5.54
August	18, 1935	.62	3.07	3.47	3.44
September	8, 1935	.95	6.24	4.68	4.94
September	26, 1935	2.40	19.60	3.97	4.50
November	27, 1935	1.20	3.12	5.64	5.90
Average		16.01	5.46	7.28

PERCOLATION

Rate of percolation of water through the prairie was determined in various habitats. Brass cylinders 4 inches in diameter and 6 inches long were dipped into hot paraffin oil so that they would make a close contact with the soil. They were then forced into the soil to a depth of 4 inches by means of a jackscrew pressing against the bed of a truck filled with rock. Water was added continuously in small quantities and the amount entering the soil per half-hour was determined. This procedure was followed for a period of 9 hours during August, 1935, at a time when the soils were relatively dry (Fig. 9).

At first the water entered all of the soils very rapidly. In the porous soil of the little-bluestem type it continued to percolate almost uniformly during the 9-hour period. A total of 14.5 inches of water was absorbed and penetrated to a depth of approximately 12 inches. The soil was moistened laterally to about 15 inches. Slightly less than 9 inches entered the soil on the low ground occupied by big bluestem. The rate of percolation through the heavy soil of the short-grass area was considerably slower. Here only 6 inches were absorbed during the 9 hours. On a short-grass strip at the base of the hill the amount was less than 3.5 inches. Water entering the soil near the shallow depression was slightly more than 3 inches in amount, but only 2 inches entered the heavy, impervious soil in the shallow depression.

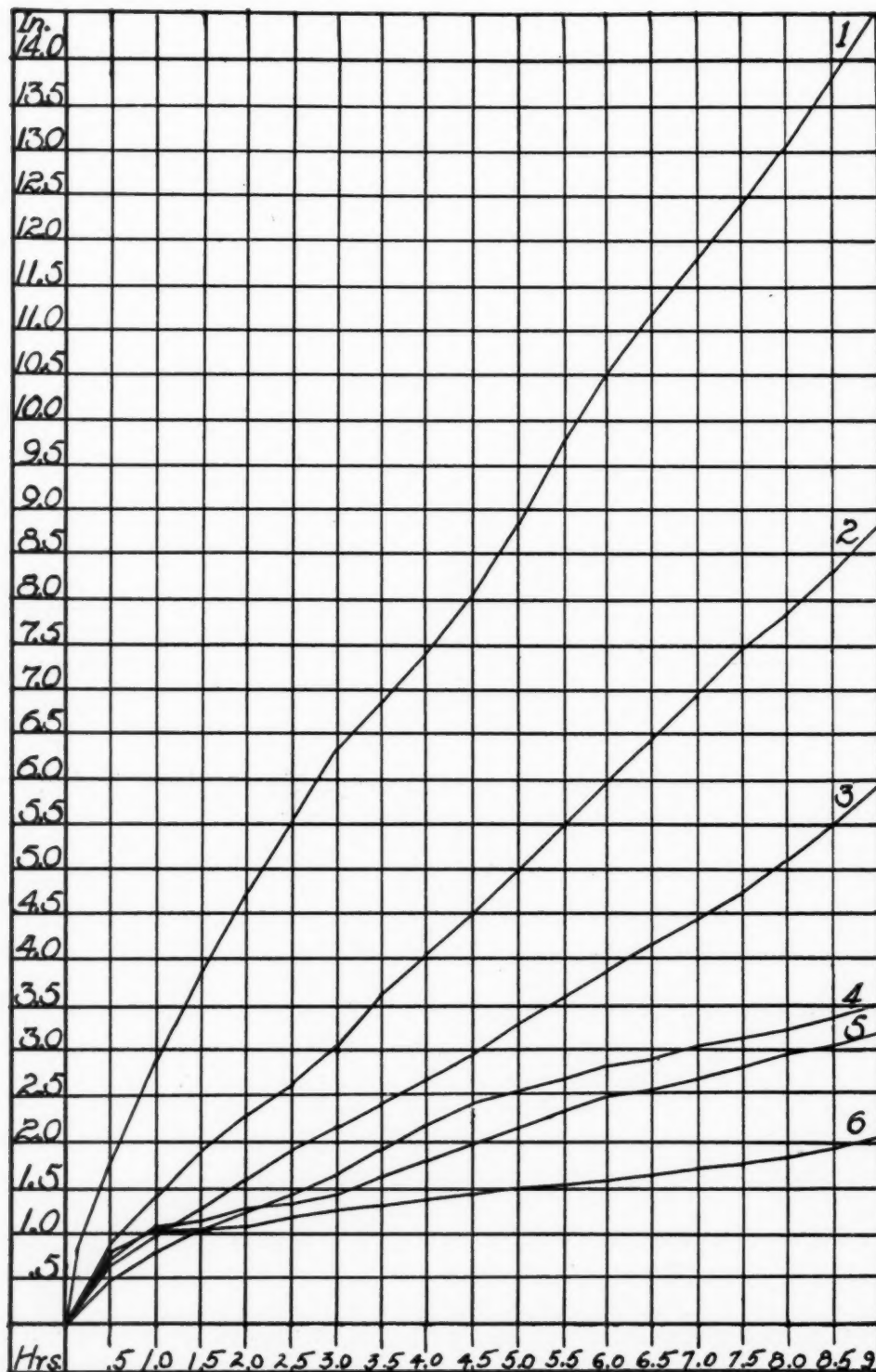


FIG. 9. Rate of percolation in inches per half-hour during a 9-hour period: (1) little-bluestem type; (2) big-bluestem type; (3) short-grass type; (4) short-grass strip at base of hill; (5) near shallow depression; and (6) in shallow depression.

PRECIPITATION AND SOIL MOISTURE

Soil samples for moisture determinations were usually taken at weekly intervals during the growing season. Hygroscopic coefficients were also determined from representative samples for each of the several depths. The percentage of soil moisture above the hygroscopic coefficient is considered to be the water available for plant growth (Alway, 1913; Alway, *et al.*, 1919).

PRECIPITATION AND SOIL MOISTURE IN SHORT-GRASS TYPE

SEASON OF 1933

Precipitation for 1933 totaled only 13.48 inches, which was 9.36 inches below normal and 14.28 inches less than that of the favorable period just preceding (Table 1). A moist spring was followed by drought in June and low rainfall during the hot summer. Conditions resulting from a very dry autumn were somewhat ameliorated by 2 inches of precipitation in December (Table 5).

Soil moisture was always available during the season of 1933 at a depth of 36 to 60 inches. This was, doubtless, residual moisture from the previous season. During the fourth week of May, no moisture was available in the

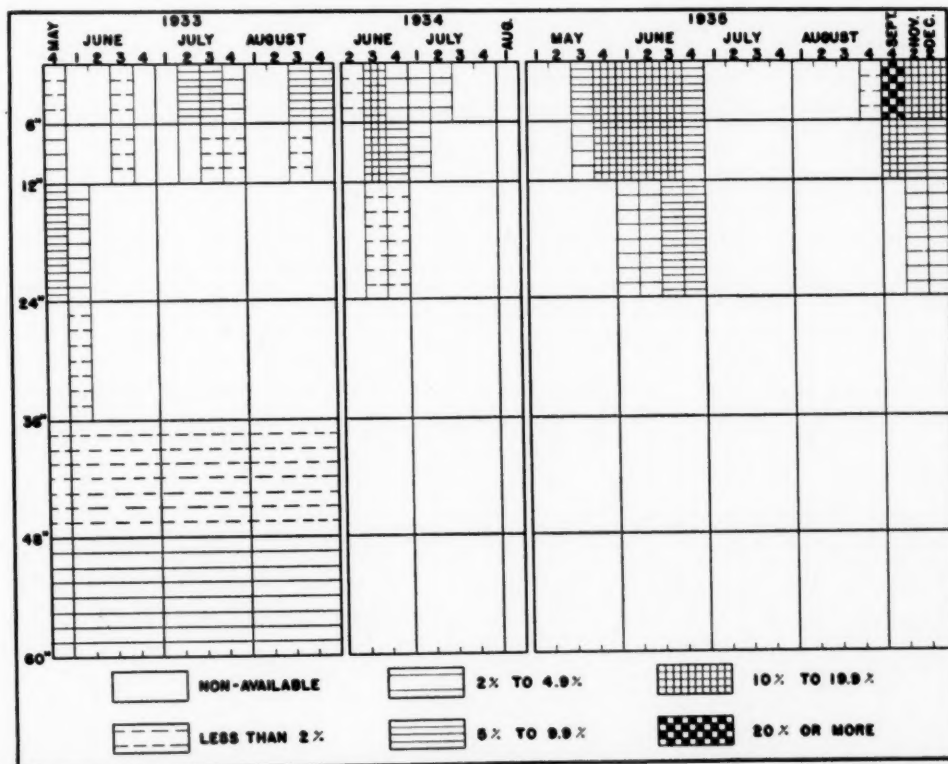


FIG. 10. Available water content of soil in the short-grass type at the several depths to 5 feet during 1933 to 1935. The hygroscopic coefficient of the soil was considered as the approximate percentage of non-available water for that depth.

third foot. During the first week of June moisture was available from 12 inches to a depth of 5 feet (Fig. 10). Beginning with the second week and throughout the remainder of the season, no moisture was available between 12 and 36 inches. The upper 12 inches, however, occasionally contained available moisture resulting from light showers. It is significant that during this season there was never as much as 10 per cent available moisture, and in most instances it was less than 5 per cent.

SEASON OF 1934

The spring of 1934 was extremely dry. The 1.55 inches of rainfall in May was dissipated in 8 showers, only one of which exceeded 0.31 inch. The 3.95 inches in June included 4 rains of 0.42 to 1.49 inches. The 6 remaining showers were so small and widely scattered as to have practically no effect upon soil moisture. July had only 2 showers, 0.15 and 0.52 inch. August with 2.21 inches had only one rainy period when any but the surface inch or two of soil was moist. This was at the end of the month when 1.35 inches of water fell during a period of two days. Six widely scattered showers, none exceeding 0.38 inch, fell in September and netted 1.59 inches of moisture. Occasional showers in October and November totaled 0.70 and 0.75 inch, respectively. The winter was extremely dry. No precipitation fell in December. The total for the year was only 13.71 inches.

TABLE 5. Annual precipitation at Hays, Kansas.

Year	January	February	March	April	May	June	July	August	September	October	November	December	Total
1933.....	0.07	0.21	0.33	2.14	2.53	0.56	1.70	1.17	2.03	0.03	0.54	2.17	13.48
1934.....	.29	1.16	.45	.37	1.55	3.95	.67	2.21	1.59	.70	.75	.02	13.71
1935.....	T	.30	.15	.21	5.26	5.12	.01	1.30	3.35	.95	2.35	.20	19.20

In May and June the soil was moist to 24 inches but the second foot contained less than 2 per cent available moisture (Fig. 10). There was only one week when the available soil moisture was more than 10 per cent and this was in the first 12 inches. Soil moisture below 2 feet was non-available during the entire season and water from rains of early summer was quickly dissipated. By the third week of July and throughout the remainder of the season there was no moisture available to a depth of 5 feet.

SEASON OF 1935

January of 1935 had no precipitation. The greatest precipitation, 0.30 inch, of the following three months occurred in February. It had no effect upon replenishing soil moisture. Thus from October 18, 1934, to May

11, 1935, there was no efficient precipitation. The drought was broken by good, well-distributed showers beginning on May 11 and extending to June 28. The total rainfall for May was 5.26 inches, and June had 5.12 inches. No rain fell during July. Of the 5 showers in August (total 1.3 inches) only one, 0.52 inches on August 20, moistened the surface of the parched soil. Thus seven weeks of excellent conditions for growth were followed by seven weeks of drought. On September 8, 0.95 inch of rain fell, and 2.4 inches on September 26, providing a total rainfall of 3.35 inches for the month. The fall and early winter months were moderately moist and some moisture accumulated in the surface soil. Precipitation for the year was 19.20 inches.

During the early spring there was no available moisture to a depth of 5 feet. Throughout June, however, somewhat less than 10 per cent occurred in the second foot. This meager supply was quickly used by the heavy growth of vegetation, and from early July throughout August, with one exception, there was no available moisture to a depth of 5 feet. At no time during the season was there available moisture below 2 feet. The small supply of soil moisture coupled with the great demands made upon the plants by extreme atmospheric conditions resulted in heavy losses of the vegetation.

SOIL MOISTURE IN LITTLE-BLUESTEM TYPE

It was generally impossible to obtain samples of soil to a depth greater than 2 feet, because of the underlying limestone layers. The soil core was often infiltrated with small pieces of limestone. In such instances, the limestone fragments were removed before weighing.

SEASON OF 1933

Water from rains during the latter part of April, 1933, penetrated to 2 feet. The first 6 inches had between 10 and 20 per cent available moisture, and the remaining 18 inches contained between 5 and 10 per cent. Late rains maintained this condition until the middle of May when the soil became gradually drier. Surface soil moisture was exhausted late in May. During a period of 4 weeks, beginning the second week in June and continuing until the second week of July, there was never more than 2 per cent available moisture to a depth of 2 feet.

The rains of early July moistened the surface soil (Fig. 11). The upper 6 inches reached its greatest water content during the third week of July when available moisture was between 10 and 20 per cent. This moisture was soon absorbed by the vegetation and no further water was supplied during the remainder of the season except in the third week of August when two small rains again moistened the surface soil.

SEASON OF 1934

The early rains moistened the soil to the full depth of 2 feet. The greatest amount of available water was found in the upper 6 inches where it was

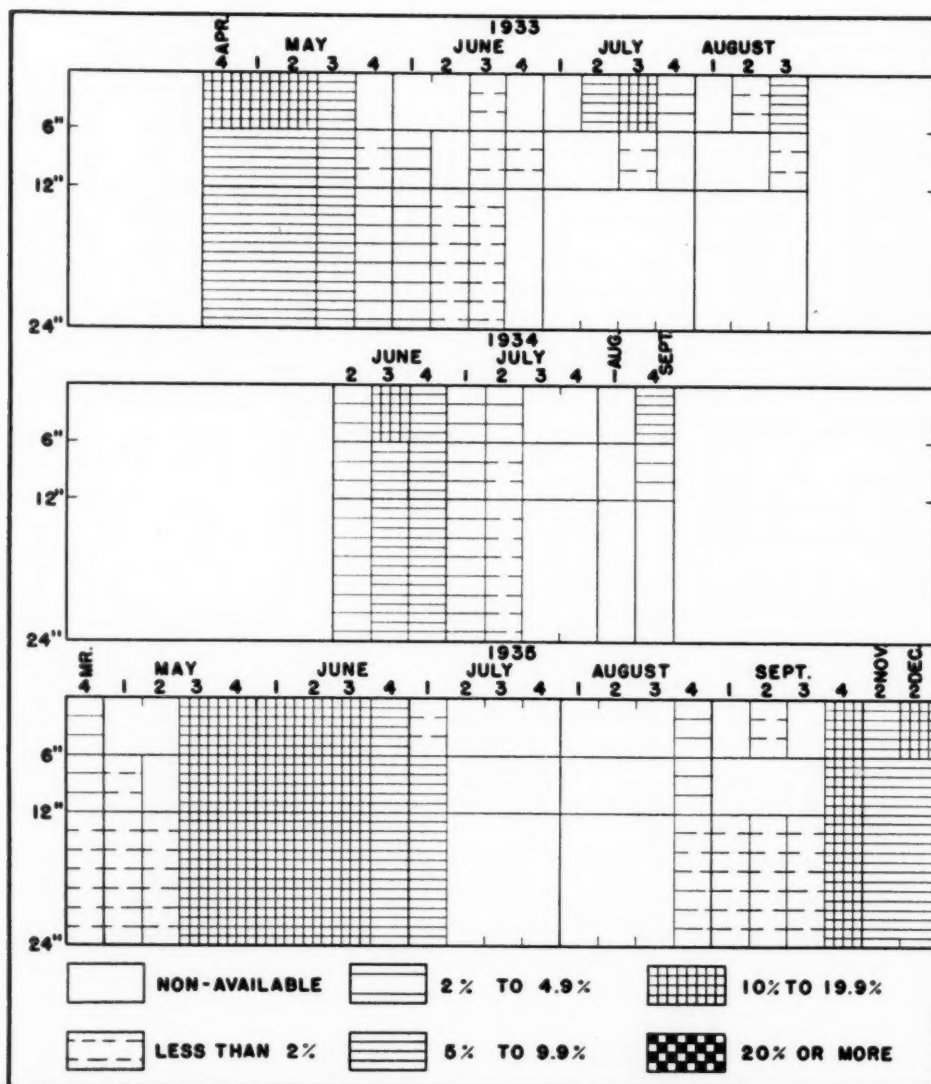


FIG. 11. Available water content of soil in the little-bluestem type to the underlying rock at a depth of 2 feet.

between 10 and 20 per cent. The amount of available moisture rapidly diminished and by the third week of July none was available to a depth of 2 feet. This extremely hot, dry period lasted until late August, when scattered showers improved conditions only slightly. During the fourth week of September the available moisture was nearly 10 per cent in the upper 6 inches and less than this amount below this depth.

SEASON OF 1935

Only a small percentage of water was stored during the previous fall. This was rapidly absorbed in early spring. The rains of May and June brought the available moisture to approximately 20 per cent. This condi-

tion was maintained for a period of 5 weeks. The rapidly growing vegetation quickly absorbed the soil moisture. From the second week of July until the fourth week of August no water was available in the upper 2 feet. The light rains during the latter part of August supplied less than 5 per cent available moisture. This amount was partially used by the renewed growth of vegetation. The soil moisture conditions were greatly improved in late September when the available supply was increased to nearly 20 per cent.

A fairly close relation was found between rainfall and available soil moisture of the first 2 feet in the little-bluestem type. The vegetation, however, was able to obtain moisture from depths below the first 2 feet. During 1934 when the short grasses had dried completely, the deeply rooted perennials growing on the sides of the hills remained fairly green and even continued to grow.

Extensive studies revealed many perpendicular and horizontal openings among the rock layers. These crevices were filled with a sandy clay of high moisture holding capacity. During the hot portion of the season when moisture was non-available in the upper soils, the available supply in these clay layers ranged from 5 to 26 per cent.

SOIL MOISTURE IN BIG-BLUESTEM TYPE

Soil moisture determinations were made in the big-bluestem habitat only during the seasons of 1934 and 1935. In every case the samples were taken to a depth of 5 feet.

SEASON OF 1934

The spring of 1934 began with 5 per cent or less available moisture in the entire 5 feet (Fig. 12). The rains of June augmented by the run-in from the surrounding slopes increased this amount to more than 20 per cent in the upper 6 inches and from 10 to 20 per cent in the deeper soil. During the remainder of the season the first 6 inches were intermittently wet and dry. Below the depth of 6 inches, however, the soil became gradually drier, and by the close of the season there was only 5 per cent or less available moisture to the 5-foot depth.

SEASON OF 1935

The dry condition of the soil in the fall of 1934 was maintained generally throughout the winter with only a slight gain. The rains of May and June replenished the water content and brought the amount available to approximately 20 per cent for the full 5-foot depth. This condition was maintained, with slight variation, until early in July. During the second week of July water became deficient in the surface 6 inches, and two weeks later this condition extended to a depth of one foot. After two more weeks no water was available to 3 feet in depth. A week later water became non-available at all depths, except that intermittent local showers moistened the surface. This condition continued until the last week of September, after

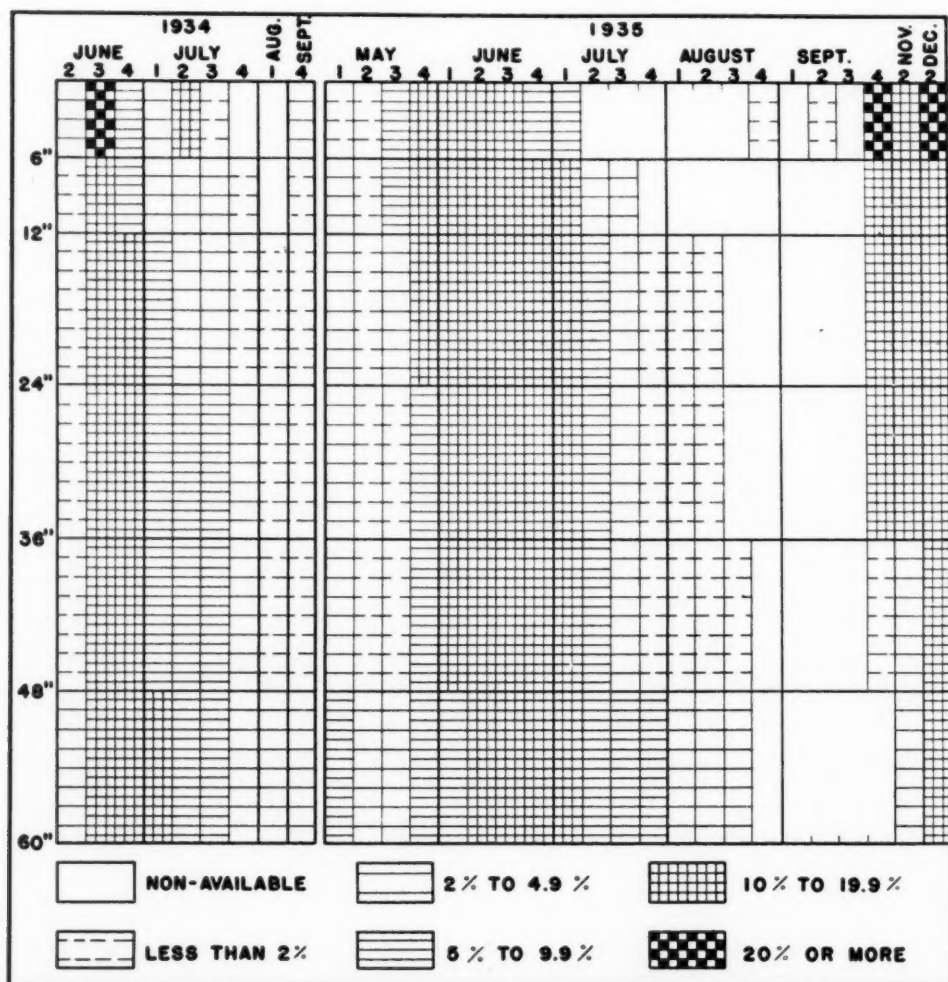


FIG. 12. Available water content of soil in the big-bluestem type at the several depths to 5 feet during 1934 and 1935.

which rains replenished both surface and subsoil moisture to a depth of 5 feet.

TEMPERATURE OF AIR AND SOIL

The temperature of the air was measured for a period of 12 weeks (June 17 to August 31) during each season. The year of 1932 was approximately normal, being the last of a 6-year moist period. During 1934 and 1935, however, there occurred the most intensive and extended drought ever recorded in the mixed prairie of Kansas.

The air temperatures of 1932 were obtained from the Fort Hays Kansas Experiment Station 2.5 miles distant. Those of 1934 and 1935 were recorded by a thermograph stationed in the short-grass area. Air temperature was recorded at a height of 4 inches above the soil surface and that of the soil at a depth of 3 inches.

The daily maximum, daily minimum, and day temperatures (6 A.M. to 8 P.M.) are averaged by weeks in Figure 13. The temperatures of 1932 and 1934 followed the same general course, being highest during a period of 2 weeks in the middle of July. The highest temperatures for 1935 were reached early in August. The daily maximum during the normal season of 1932 ranged between 80°F. and slightly above 100°F. The average was 90.9°. The daily maximum for 1934 was nearly 8° higher, ranging between 75° and 111°F. and averaging 98.1°. It is significant that the daily maximum temperatures of 1934 averaged above 100°F. during 6 weeks and above 110°F. during 2 weeks. During 1935 the daily maximum was midway between those of 1932 and 1934. It ranged between the extremes of 78° and 104°F. and averaged 94°.

The daily minimum temperature during 1932 ranged between 60° and 71°F. The average was 65.4°. During 1934 it ranged between 59° and 76°F. and averaged 67.2°. The range during 1935 was between 54° and 76°F.

The mean day temperature of 1932 was 81.2°F. It was slightly higher in 1935 (83.6°F.). During 1934, however, it was 87.1°F. which was nearly 6° higher than that of the normal season of 1932.

Air and soil temperatures for 1934 are compared in Figure 14. The average daily maximum of the air was from 2° to 5°F. higher than that of the soil until July 23, after which there were no consistent differences. The mean day temperatures were consistently 1° to 3° lower than those of the soil until July 16. Thereafter there were continuous variations. The average daily minimum soil temperature after June 18, however, was always 10° to 15° higher than that of the air. During the hottest weeks this lowest soil temperature was 86° and 88°F.

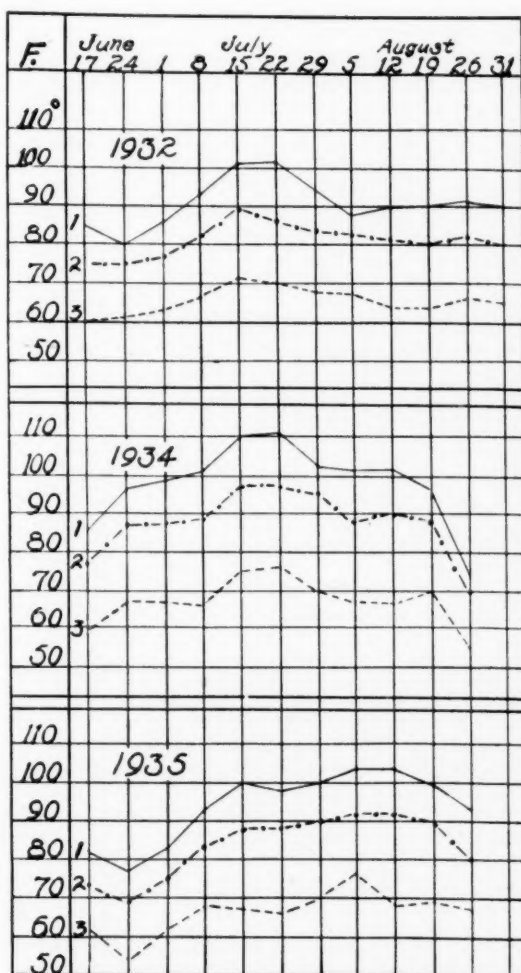


FIG. 13. (1) Average daily maximum temperature; (2) average day temperature; and (3) average daily minimum temperature by weeks during the several growing seasons.

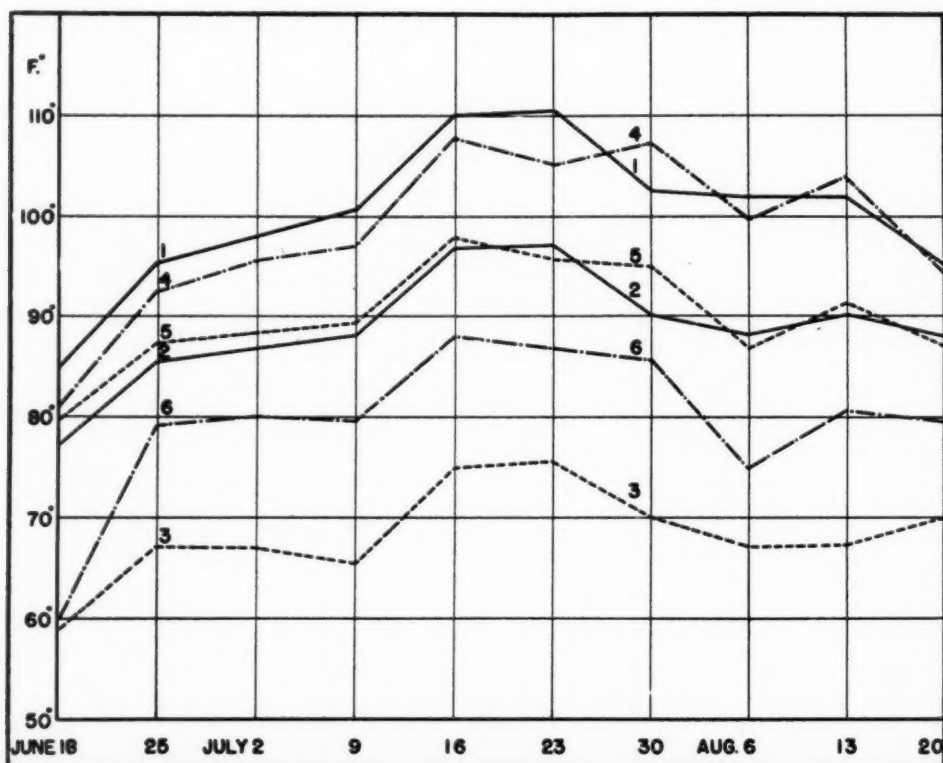


FIG. 14. Temperatures of air and soil by weeks during 1934: (1) average daily maximum temperature; (2) average day temperature (6 a.m. to 8 p.m.); (3) average daily minimum temperature; (4) average daily maximum soil temperature at 3-inch depth; (5) average daily soil temperature; and (6) average daily minimum soil temperature.

RELATIVE HUMIDITY

Relative humidities were determined at various intervals during the growing season of 1934 by means of a cog psychrometer. Deficient rainfall and high temperatures caused the air to become extremely dry especially during late mornings and afternoons. A large number of readings, made between 2 and 4 P.M. at various places in the prairie, ranged from 9 to 34 per cent. Readings made between 8 and 9 A.M. in the same locations but on different days varied from 43 to 60 per cent.

Humidities were determined by a hygrograph operated in the short-grass area during 1935. The relatively cool, moist conditions during late May and June resulted in high humidity until early in July when, because of summer drought, the decrease was very abrupt (Fig. 15). Low humidity prevailed until near the middle of August when rains replenished the supply of moisture to both soil and air.

The daily minimum humidity from June 17 to August 26 ranged from 21 to 63 per cent and averaged 39.3 per cent. The daily maximum relative humidity ranged from 63 to 97 and averaged 83.5 per cent. The mean day

humidity (6 A.M. to 8 P.M.) ranged from 40 to 74 per cent. The average was 51 per cent.

EVAPORATION

The rate of evaporation was measured during three seasons in the shortgrass and little-blue-stem habitats, and during 1934 and 1935 in the big bluestem. Livingston's standardized, white, spherical atmometers, each fitted with a non-absorbing device, were operated in pairs at a height of 3 inches above the soil surface. A second pair was also operated in each of the taller grass types at one-half the height of the grasses; the maximum height was 6 inches in the little-bluestem and 8 in the big-bluestem type. Readings were made weekly and reduced to those of standard atmometers (Fig. 16).

Evaporation in the short-grass habitat during 1933 fluctuated between the extremes of 40 and 89 cc. per day. In 1934 the extremes were even greater; the lowest daily loss was only 36 cc. but the highest reached 138 cc. during the third week of July when the air was unusually hot and dry. In 1935 the high average daily loss of 98.4 cc. occurred early in May but decreased to only 18 to 30 cc. with the occurrence of the spring rains. The low point of daily loss (12.4 cc.) was reached during the fourth week of June, which was one of the high periods of evaporation during the two previous seasons. When the summer drought appeared, the daily loss increased rather rapidly and reached a maximum of 88.4 cc. during the first week of August.

Evaporation in the little-bluestem type followed the same general course as it did in the short grass. The loss, however, was usually from 10 to 20 cc. per day less, and even 30 cc. less during certain weeks. Average daily evaporation during 1933 ranged from 15 to 54 cc. It was 19 to 88 cc., however, during the drier year of 1934. The greatest loss in 1934 occurred late in May before there was any protection from the surrounding vegetation. Losses

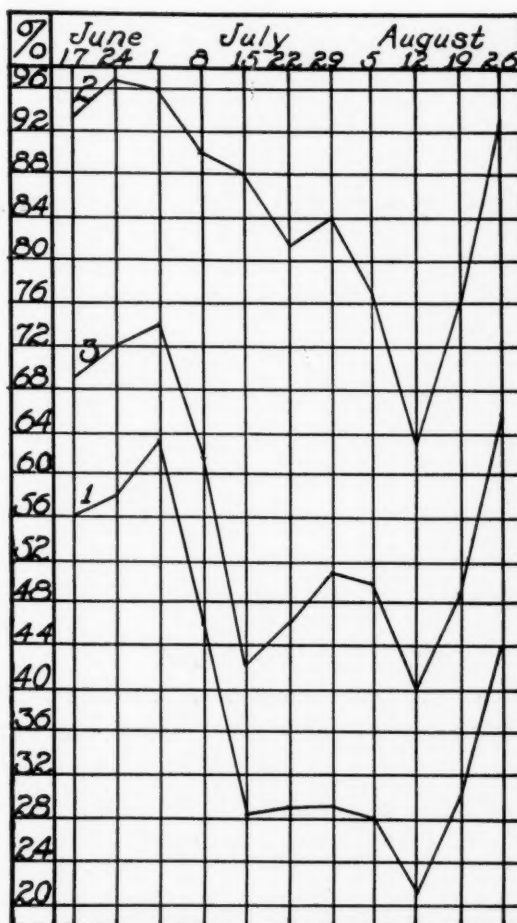


FIG. 15. (1) Average daily minimum humidity; (2) average daily maximum humidity; and (3) mean day humidity during 1935.

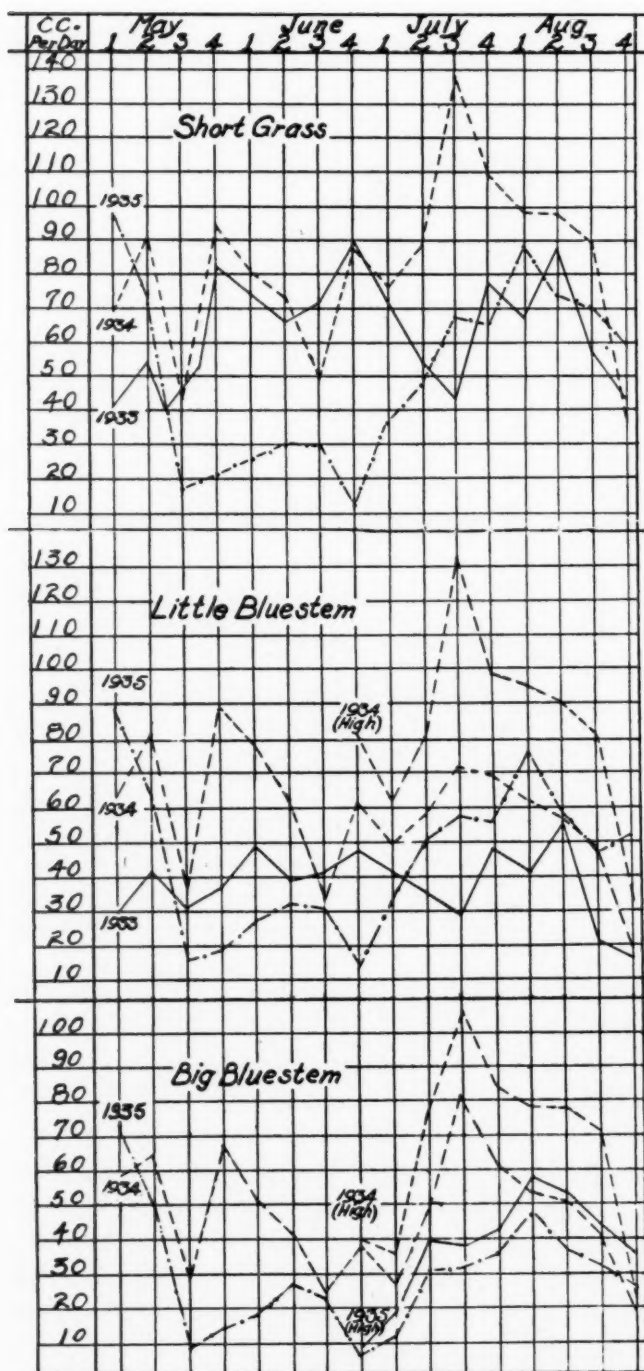


FIG. 16. Relative rates of evaporation in the several habitats during three successive years. All atmometers were placed at a height of 3 inches above the soil surface except those from which the data (graphs) are designated as "high." These were operated at one-half the height of the vegetation.

from the atmometers placed at one-half the height of the vegetation were 12 to 60 cc. greater than those at the 3-inch level (Fig. 16). The evaporation during 1935 followed the same general course in the little bluestem as it did in the short-grass type, but was usually slightly lower. The growth of vegetation was so poor that there was no significant difference between the loss from the atmometers placed at the 3-inch level and those operated at half the height of the grasses.

Evaporation in the big bluestem was considerably less than that in either the short grass or little bluestem. During 1934, it ranged between 5 and 20 cc. per day less than that in the little bluestem. The average daily evaporation was relatively high during the first week of May (59.1 cc.) due to the small amount of protection afforded by the surrounding vegetation. During the remainder of the season losses at the 3-inch level fluctuated between the extremes of

25 and 81 cc. per day. Daily evaporation rate increased rapidly with increased height of atmometers from 35 cc. during the first week of July to 106 during the third. This exceeded the average daily rate at the 3-inch height by 9 to 25 cc.

During 1935, evaporation was relatively high at the beginning of the season but decreased rapidly to 5.4 cc. in the fourth week in June. The maximum of 47 cc. was attained during the first week of August when the summer drought was most intense. Atmometers placed at half the height of the grasses lost 2 to 10 cc. more than those at the 3-inch level.

The differences in rates of evaporation at the three stations are shown for the season of 1934 in Figure 17. The sequence, in general, is representative of both the preceding and the following season. The much higher evaporation rates from the short-grass area, especially during great stress, is clearly revealed, as is also the lower rate among the taller plants of the more sheltered big-bluestem community.

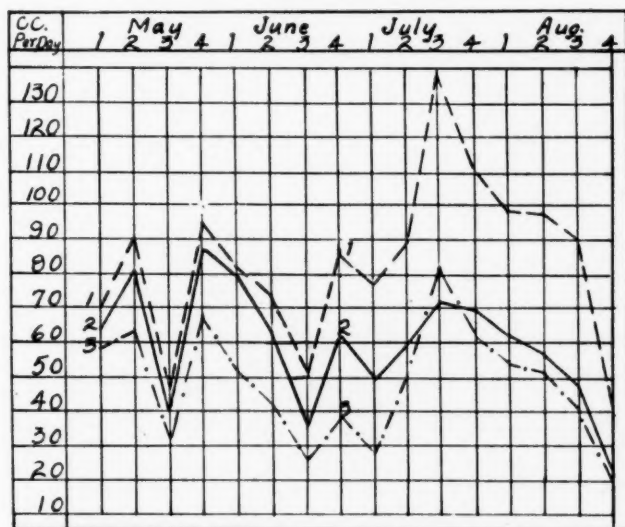


FIG. 17. Average daily evaporation by weeks during 1934 from (1) short-grass, (2) little-bluestem, and (3) big-bluestem habitats, respectively. Atmometers were placed at a height of 3 inches above the surface of the soil.

WATER LOSS FROM PHYTOMETERS

Phytometers were used during 1934 and 1935 to determine water loss from unit areas of each of the three types of vegetation. They were prepared by placing typical blocks of sods, one square foot in area and 18 inches deep, into heavy, cylindrical, metal containers of 1.5 cubic feet capacity. This was done without disturbing the vegetation or the structure of the soil. One phytometer of each vegetational type was placed in the soil in each of the three grassland communities in such a manner that the ground level of the experimental vegetation was the same as that surrounding the container. The rim of the container projected one-fourth inch above the soil surface. In preparing the phytometers, the moisture content of the soil was brought to an approximate optimum of 30 per cent and the total weight was then determined. Loss of water was ascertained by weighing at weekly intervals at which time enough water was added to replace the amount lost during

the previous week. These data are recorded as pounds per square foot per day (Fig. 18).

The loss of water was usually greatest from phytometers placed among the short grasses, and least from those located in the big-bluestem type. Moreover, losses from the big bluestem were greatest and those from the short grasses usually least in each of the three plant communities. The short grass had an average daily loss of 0.4 to 1.78 pounds per square foot in its

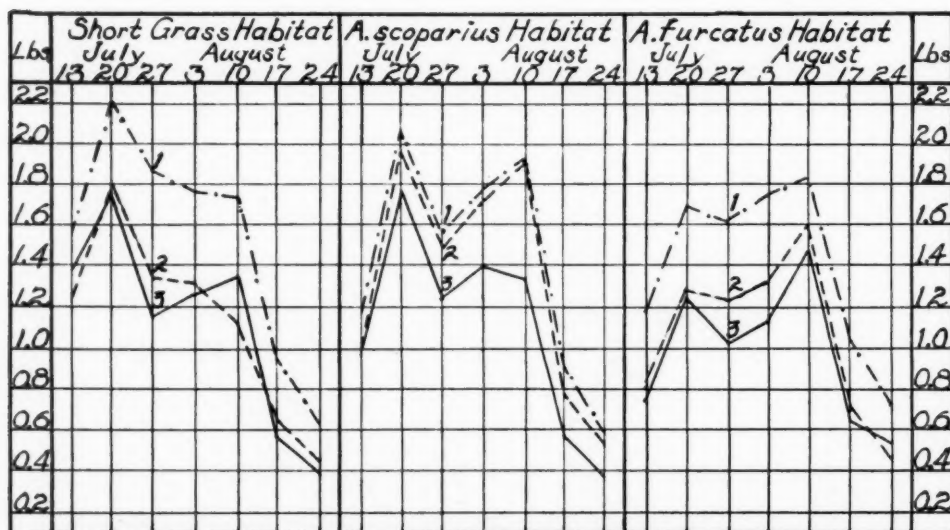


FIG. 18. Water loss from plant phytometers: (1) big bluestem; (2) little bluestem; and (3) short grass.

own habitat, 0.39 to 1.75 pounds in the little-bluestem type, and 0.43 to 1.48 pounds in the big-bluestem habitat.

The loss of water from the little-bluestem phytometer in the short-grass type was nearly the same as that from the short-grass phytometer. Water loss from the little-bluestem phytometer in its own habitat ranged between 0.51 and 1.99 pounds per square foot, which was considerably greater than that from the short-grass phytometer similarly placed. In the big-bluestem type the little bluestem lost 0.44 to 1.6 pounds. Losses from the big-bluestem phytometers in the same sequence were 0.62 to 2.2, 0.6 to 2.0 and 0.7 to 1.8 pounds.

Translated into tons per acre per day, the average water losses through transpiration and surface soil evaporation during the hottest period of 4 weeks were as follows: Short grasses in the short-grass area 30 tons; in the little-bluestem type 31 tons; and in the big-bluestem type 24 tons. In the same sequence water losses from little bluestem were 30, 38, and 29 tons; those from the big bluestem were 51, 39, and 37 tons per acre. It should not be inferred that the unwatered vegetation surrounding the phytometers yielded similar losses. The data do reveal the enormous amounts of water

lost from natural prairie vegetation during periods of stress when soil moisture is available.

THE VEGETATION

Studies on the vegetation were made almost continuously throughout the period of 4 years. The selected area was visited regularly, often daily during the growing season and at frequent intervals during the dormant one. Although this report is limited to the 750-acre tract, numerous other areas of similar mixed prairie have been studied in order to obtain a better background for the intensive work. The writer is a native of Kansas and was well acquainted with the prairie flora before this study was begun.

List quadrats and especially permanent chart quadrats were used extensively. More than 150 of the latter alone have been made. Transects were also employed. Bisects were used extensively. Trenches, 3 to 13 feet deep and aggregating nearly 400 feet in length, were excavated, often through the limestone rock, to ascertain the relations of underground plant parts to the rock crevices and soil. Major attention was given to community relationships both above and below ground and this involved detailed study of the ecology of the more important species.

BULBILIS-BOUPELOUA TYPE

The appearance of the short-grass vegetation is that of a well-grazed meadow except for the presence of certain taller grasses and forbs. These are typically scattered throughout or, where conditions are more favorable, they may become locally the conspicuous features of the landscape. The two short grasses (*Bulbilis dactyloides* and *Bouteloua gracilis*) alone furnish fully 80 per cent of the vegetation. The foliage of these grasses is only 3 to 5 inches high and of a dark green color when moisture is plentiful. With the advent of drought the grasses become bleached to various shades of yellowish green and finally to a light gray. When drought is broken they soon resume the original green color. These changes occur almost every season. The "cured" condition of dormancy is the prevalent one during years of drought.

The density of vegetation varies from that of the usual closed-mat type, in which 70 to 90 per cent of the soil is covered, to the open-mat type of poorer soils where only 20 to 30 per cent is clothed during a season of normal precipitation. The foliage cover of the short grasses during dry years scarcely exceeds the area of the plant bases but is somewhat greater under favorable conditions for growth.

Permanent meter quadrats were located in representative areas in each of the communities and charted in the fall of 1932, 1934, and 1935. The pantograph-chart method was used in making the quadrats. The short grasses as well as the open sod of the little-bluestem type lend themselves readily to this method of study. The ground or basal cover represents that portion of the soil occupied by the basal cross section of the crowns, by

prostrate stems, and by stolons of living plants. Where such plant parts were less than 2 centimeters distant, the area was considered as being fully occupied. Each chart had an area of 2.25 sq. dm., and a ratio to the length of the quadrat of 1 to 6.66. The percentage of basal cover occupied by each species was determined from the charts by means of planimeters.

A typical unit area from the closed-mat type is shown in Figure 19. This square meter was charted in the fall of 1932. The basal cover of the short grasses was 86 per cent. The open places are bare ground. *Aristida purpurea*

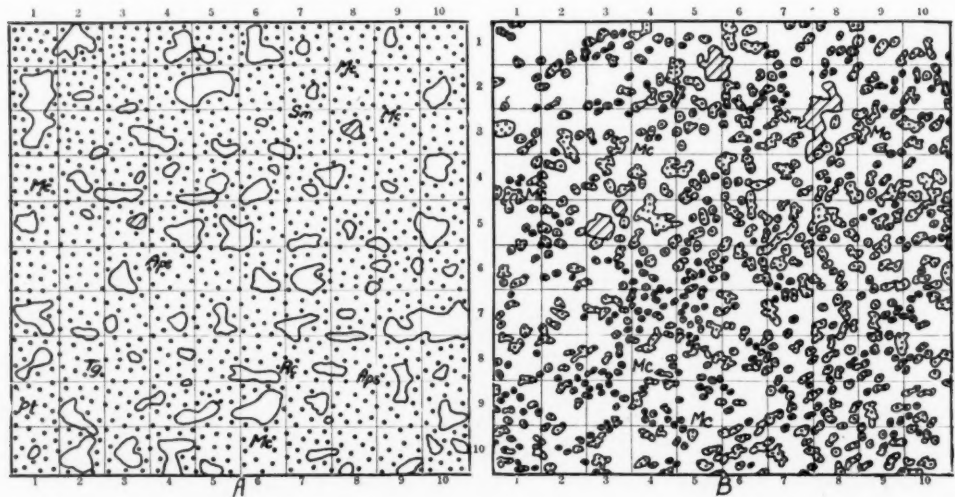


FIG. 19. (A) Typical closed-mat type of short-grass cover which predominated in 1932, before the great drought. A nearly equal mixture of *Bouteloua gracilis* and *Bulbilis dactyloides* (stippled) composed 86 per cent, and *Aristida purpurea* (hatched) about 0.5 per cent of the basal cover: (B) Same quadrat after the great drought of 1934. The cover of short grasses was reduced to 32 per cent.

occupied less than 0.5 per cent of the ground cover. The same area was charted again in the spring of 1935 (Fig. 19). The basal cover had decreased to 32 per cent. *Aristida* had made a slight gain. *Solidago mollis* and *Malvastrum coccineum* were the only forbs able to survive the drought of 1933 and 1934.

To determine changes in plant population other than the dominants, a meter quadrat was made in a typical short-grass area. The position and abundance of each plant was determined in the fall of 1932 (Fig. 20). By 1935 all the plants except the two dominant grasses had disappeared. *Malvastrum coccineum* had entered the quadrat sometime during the three years.

The open-mat type of vegetation growing in the shallow depressions was also charted in the fall of 1932 and again late in 1935 (Fig. 21). The basal cover of the short grasses was originally 33 per cent. This was reduced to 2.6 per cent by the fall of 1935. There was, however, a great increase in the number and species of forbs.

These quadrats indicate that the composition of the short-grass community was greatly modified by the drought of 1933 to 1935. Extensive

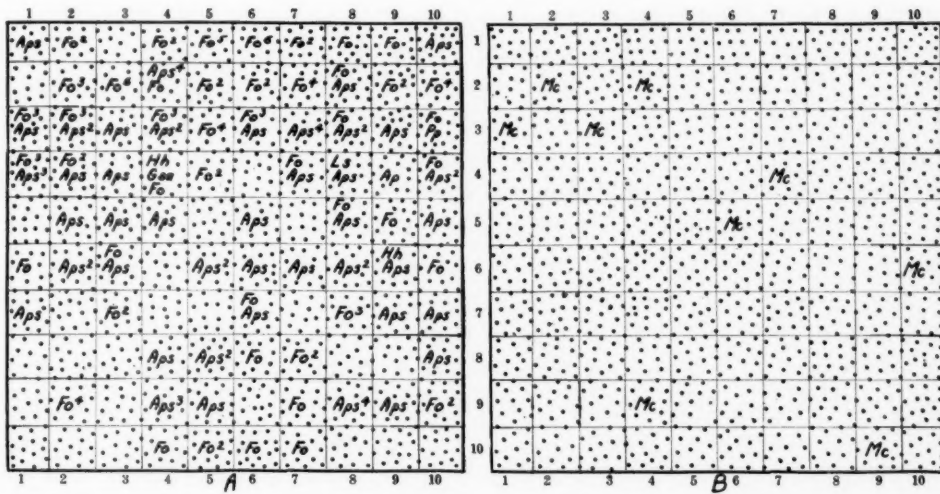


FIG. 20. (A) Short grass (considered as a continuous cover) with an abundance of forbs and annual grasses, charted in 1932. *Ambrosia psilostachya* (Aps); *Festuca octoflora* (Fo); *Plantago purshii* (Pp); *Gutierrezia sarothrae* (Gsa); *Hedeoma hispida* (Hh); *Linum sulcatum* (Ls); and *Aristida purpurea* (Ap). The exponent near the symbol represents the number of plants found in each square decimeter. (B) Same quadrat in fall of 1935. *Malvastrum coccineum* (Mc).

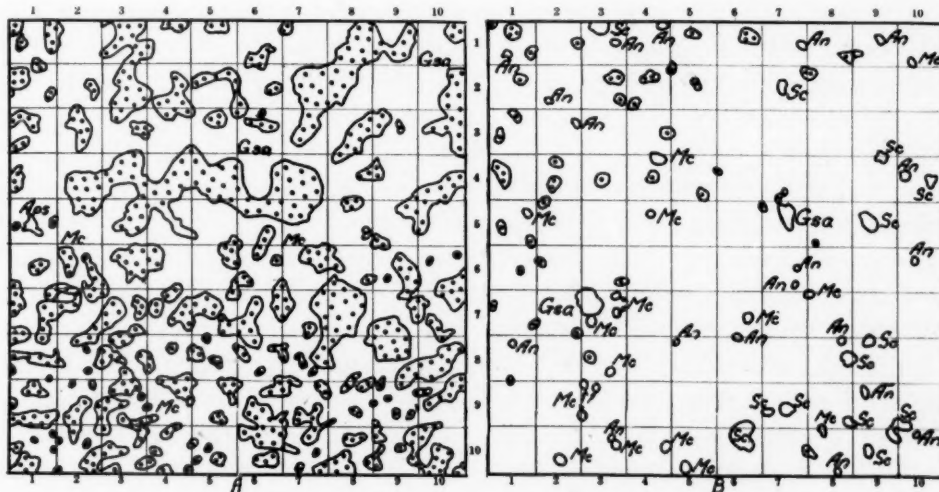


FIG. 21. (A) Square meter area in a shallow depression showing the typical open cover of short grasses (stippled) in 1932. (B) The same area after the great drought. The short grasses have nearly disappeared. This was followed by the invasion of *Sporobolus cryptandrus* (Sc).

studies reported elsewhere (Weaver and Albertson, 1936) show that losses in the open-mat type of ungrazed short-grass cover were 70 to 80 per cent. In the closed type they were usually relatively small, although certain native forbs entirely disappeared. These data, as well as those from which the original composition of the vegetation was calculated, are based on scores of long-time permanent quadrats similar to those described (cf. Savage and Jacobson, 1935).

Stolons of *Bulbilis dactyloides* rapidly reclaimed bared areas when moisture was available for growth. Lengths of 6 to 18 inches were frequently attained. They grew at the rate of one inch or less per day until overtaken by drought. Then, because of the shallow rooting at the distal nodes, they usually died back, sometimes to only one-third their length but often entirely.

The short grasses resume growth early in March although some well-protected leaves in the crowns remain green all winter. Early in May the new stolons of buffalo grass may be seen. Flowering begins by the middle of the month and fully matured fruits may be found early in June. Blue grama grass blossoms several weeks later. It spreads only slowly vegetatively underground, but seeds prolifically. The seedlings are usually numerous, especially in bared areas. While the pistillate flowers of the buffalo grass are found intermixed with leaves, the staminate spikes extend 1 to 3 inches above the foliage. Flower stalks of blue grama grass attain a height of 8 to 15 inches above the soil surface, depending upon the water supply.

The relative proportion of the two dominants varies considerably under different conditions. The grasses usually occur in mixed stands and the percentage of each component can be determined only upon careful examination. In the fall of 1931, sods 8 inches square were removed, the soil carefully washed away, and the culms separated and counted. The number of stems of each species ranged between 1,404 and 1,620 per square meter. On another occasion, the culms on one square meter were counted. There were 1,675 stems of blue grama grass and 1,624 of buffalo grass.

Approximately 95 per cent of the prairie species are long-lived perennials, a condition that prevails in the other communities as well. Certain annuals, however, although of small stature are so abundant as to be conspicuous and important. Chief among these are *Hordeum pusillum*, *Festuca octoflora*, *Plantago purshii*, and *P. spinulosa*. All are interstitial species but may grow thickly in the short-grass sod or cover bare areas completely where drought has destroyed the dominant grasses. Hence, in early spring the yellow-green carpet of *Hordeum* and *Festuca* may be conspicuous. Later it becomes yellow as these small annuals mature and die. Elsewhere spots or patches of silvery gray reveal the abundance of the plantains.

Taller grasses where thickly grouped form a distinct upper layer, but these bunch grasses are usually not abundant. The most important are *Aristida purpurea*, *Andropogon scoparius*, *Bouteloua curtipendula* and *Sitanion elymoides*. These tall grasses, even if not abundant, are conspicuous as are also the prickly pear, *Opuntia humifusa*, societies of goldenrods (*Solidago mollis*), false red mallow (*Malvastrum coccineum*) and widely spaced plants of *Psoralea tenuiflora*.

Although an upper story of plants is often sparse, two layers of vegetation are usual. Besides the short grasses numerous rosette and mat-forming plants or low annuals occur near the soil. Most conspicuous among these are *Leucelene ericoides*, *Antennaria campestris*, *Diaperia prolifera*, *Oxalis stricta*,

Draba caroliniana, *Astragalus shortianus* and *Hedeoma hispida*. Aside from the taller species already noted, *Gutierrezia sarothrae* and *Lacinaria punctata* are common to abundant in the upper layer.

Layering underground is well marked. The general root depth of nearly all of the grasses is 4 to 5 feet. Many subdominants, especially those blossoming in spring or early summer, are as shallowly or more shallowly rooted than the grasses. Thus there are formed two more or less distinct layers underground. A third, consisting almost entirely of roots of the most important late blooming forbs, extends to a depth of 6 to 9 feet.

As in the mixed prairie generally the most important plant families, aside from the grasses, are the Compositae, Papilionaceae, and Onagraceae. There are, as in the true prairie eastward, four rather distinct seasonal aspects. The prevernal of March and early April has the fewest species; the vernal, extending to late May, has a wealth of low-growing flowers. Plants of the estival and autumnal aspects are usually much taller, undoubtedly an adjustment to the light relation where they grow in competition with tall grasses. While many of the species are also found in the other mixed-prairie communities as well as eastward in true prairie, yet the more xeric nature of this grassland is evident.

Poa pratensis, which is a general invader of true prairie (Weaver and Fitzpatrick, 1934), does not occur. *Fragaria virginiana*, *Phlox pilosa*, *Hypoxis hirsuta*, *Galium tinctorium* and a large group of other species are not found here. Moreover, societies of those that do occur are not so extensive as in a climate of greater rainfall, and the individuals are dwarfed. Finally, the more xeric conditions are shown by an abundance of distinctly western plants such as *Sideranthus spinulosus*, *Gutierrezia sarothrae*, *Malvastrum coccineum*, and *Solidago mollis*.

An intensive study of the distribution, extent, and development of the chief societies of each major community was abandoned after the first year because of the disturbances resulting from the continuous drought.

The grasses and forbs constituting the short-grass community are grouped according to their ecological importance in Table 6. A few that are found only rarely are not included.

TABLE 6. PLANTS OF THE SHORT-GRASS HABITAT

Dominant species
<i>Bouteloua gracilis</i> (H. B. K.) Lag.
<i>Bulbilis dactyloides</i> Raf.
Principal species of grasses and sedges
<i>Agropyron smithii</i> Rydb.
<i>Andropogon scoparius</i> Michx.
<i>Aristida purpurea</i> Nutt.
<i>Bouteloua curtipendula</i> (Michx.) Torr.
<i>Carex praeegracilis</i> W. Boott.
<i>Sitanion elymoides</i> Raf.

Grasses of secondary importance

Alopecurus carolinianus Walt.
Andropogon furcatus Muhl.
Distichlis stricta (Torr.) Rydb.
Festuca octoflora Walt.
Hordeum pusillum Nutt.
Munroa squarrosa (Nutt.) Torr.
Sporobolus asper (Michx.) Kunth
Sporobolus cryptandrus (Torr.) A. Gray

Principal species of forbs

Ambrosia psilostachya DC.
Anemone caroliniana Walt.
Antennaria campestris Rydb.
Aster multiflorus Ait.
Astragalus missouriensis Nutt.
Astragalus mollissimus Torr.
Astragalus shortianus Nutt.
Cirsium undulatum (Nutt.) Spreng.
Gaura coccinea Nutt.
Grindelia squarrosa (Pursh) Dunal
Gutierrezia sarothrae (Pursh) Britton and Rusby
Kuhnia glutinosa Ell.
Lacinaria punctata (Hook.) Kuntze
Leucelene ericoides (Torr.) Greene
Lithospermum linearifolium Goldie
Malvastrum coccineum (Nutt.) A. Gray
Merioliix serrulata (Nutt.) Walp.
Opuntia humifusa Raf.
Plantago purshii R. and S.
Plantago spinulosa Decne.
Psoralea tenuiflora Pursh
Ratibida columnaris (Sims) D. Don.
Sideranthus spinulosus (Pursh) Sweet
Solidago glaberrima Martens
Solidago mollis Bartl.
Sophora sericea Nutt.
Thelesperma gracile (Torr.) A. Gray

Forbs of secondary importance

Accrates auriculata Engelm.
Acerates viridiflora (Raf.) Eaton
Achillea millefolium L.
Allionia linearis Pursh
Allium nuttallii S. Wats.
Agoseris cuspidata (Pursh) D. Dietr.
Asclepias pumila (A. Gray) Vail
Astragalus crassicaipus Nutt.
Cerastium brachypodum (Engelm.) B. L. Robinson
Cheirinia aspera (Nutt.) Rydb.
Delphinium carolinianum Walt.
Diaperia prolifera Nutt.

Draba caroliniana Walt.
Galpinsia lavendulaefolia (T. and G.) Small
Hedeoma hispida Pursh
Hymenopappus corymbosus T. and G.
Linum compactum A. Nels.
Linum sulcatum Riddell
Lygodesmia juncea (Pursh) D. Don.
Myosurus minimus L.
Neomamillaria radiosa (Engelm.) Rydb.
Oxalis stricta L.
Parosela enneandra (Nutt.) Britton
Pentstemon albidus Nutt.
Phellopterus montanus Nutt.
Polygala verticillata L.
Psoralea cuspidata Pursh
Psoralea esculenta Pursh
Senecio plattensis Nutt.
Spermolepis patens (Nutt.) Robinson
Stenosiphon linifolium (Nutt.) Britton
Verbena bracteosa Michx.

UNDERGROUND PARTS IN RELATION TO TOPS

In order to determine the ecological relationships of various species it was necessary to study the underground parts as well as those above the soil. Trenches about 30 inches wide and sufficiently deep to include the entire root system were dug at various places in the prairie during the summers of 1933, 1934, and 1935. Ice picks were used to remove the coarse roots of the forbs, and water from a spray was employed to wash the soil from the relatively fine roots of the grasses. After the roots were exposed they were carefully drawn on ruled paper to a scale of 2 inches to 1 foot.

The root extent of the three grasses most commonly found in this habitat are shown in Figure 22. Both blue grama and buffalo grass have roots that are very fine and occupy the major portion of the soil to a depth of approximately 5 feet. The roots of wire grass are somewhat coarser and the root system lacks the abundant laterals so pronounced in its short-grass competitors.

The rapid growth of *Aristida purpurea* in spring, the early period of flowering, and its greater height are all advantageous. Where abundant it produces considerable shade and the developing panicles give a purple cast to the landscape. The large, three-awned fruits are scattered widely by the wind and the seeds are planted by means of the hygroscopic awns. Seedlings are often abundant both in fall and spring.

The root systems of both little bluestem and slender grama grass are similar in depth, spread, and other respects to those of the wire grass. That of *Sitanion elymoides* is somewhat shallower. All are long-lived and of much greater stature than the short grasses. *Carex prae-gracilis* is a grass-like, sod-forming perennial whose root system is almost confined to the sur-

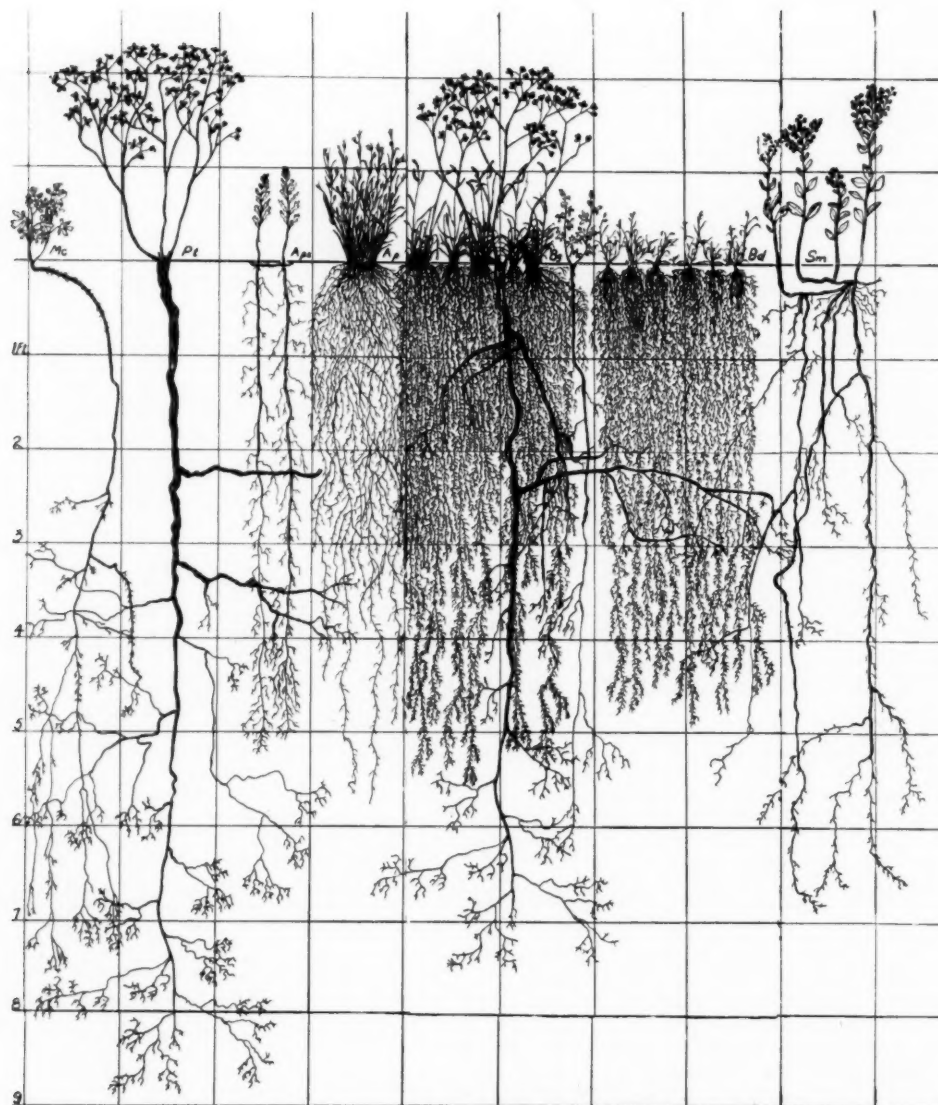


FIG. 22. Bisect showing relations of roots and tops of grasses and forbs in a typical short-grass area. *Malvastrum coccineum* (Mc); *Psoralea tenuiflora* (Pt); *Ambrosia psilostachya* (Ap); *Aristida purpurca* (Ap); *Bouteloua gracilis* (Bg); *Bulbilis dactyloides* (Bd); and *Solidago mollis* (Sm). None of the forbs characteristic of the ground layer are shown here. Note the very definite root layer formed by the grasses and the deeper one by coarse forbs.

face foot. This shallow rooting habit may be correlated with its very early development in spring before the dominants renew growth. It flowers early and is thereafter inconspicuous despite its abundance.

The more important forbs are usually much more deeply rooted than the grasses (Fig. 22). *Malvastrum coccineum*, a low-growing perennial with salmon-colored flowers, occurs singly or in societies. The main root may remain unbranched to a depth of 3 feet where it divides into laterals that continue far into the subsoil. It is extremely drought resistant.

Psoralea tenuiflora extends above the level of even the taller grasses and its strong tap root normally penetrates far beyond that of the grasses and most other forbs. In fact, it absorbs little in the first few feet of soil. Greater abundance of this legume indicates increased subsoil moisture.

Ambrosia psilostachya, the perennial ragweed, commonly invades the short grasses from the disturbed places along the slopes. Distant migration is by seeds and local spreading by rhizomes in the surface two inches of soil. The roots are rather uniformly branched and extend to a depth of 3 to 6 feet.

Solidago mollis reaches a height of 6 to 24 inches. It is found sometimes singly but usually in societies 6 to 10 or more feet in diameter. Propagation is mainly by rhizomes. The yellow, fleshy roots often reach a depth of 7 feet.

Kuhnia glutinosa is widely scattered but is never abundant (Fig. 23). It normally occurs as single plants with several branches that reach a height of 8 to 12 inches. This is in sharp contrast to the larger plants with numerous branches that are found regularly in true prairie. The large, light-colored tap root often penetrates the soil to a depth of 12 to 14 feet.

Gutierrezia sarothrae grows from a woody base and remains green through most of the winter. The height seldom exceeds 10 inches. Myriads of small, yellow flowers normally cover this bushy perennial during late fall. There is usually much branching of the roots near the surface after which they penetrate to a depth of 4 to 5 feet (Fig. 24).

Solidago glaberrima occurs only occasionally on gentle slopes or in low places. The golden-colored panicles are formed on stems 8 to 12 inches high in late July to September. Propagation is chiefly by rhizomes and so-

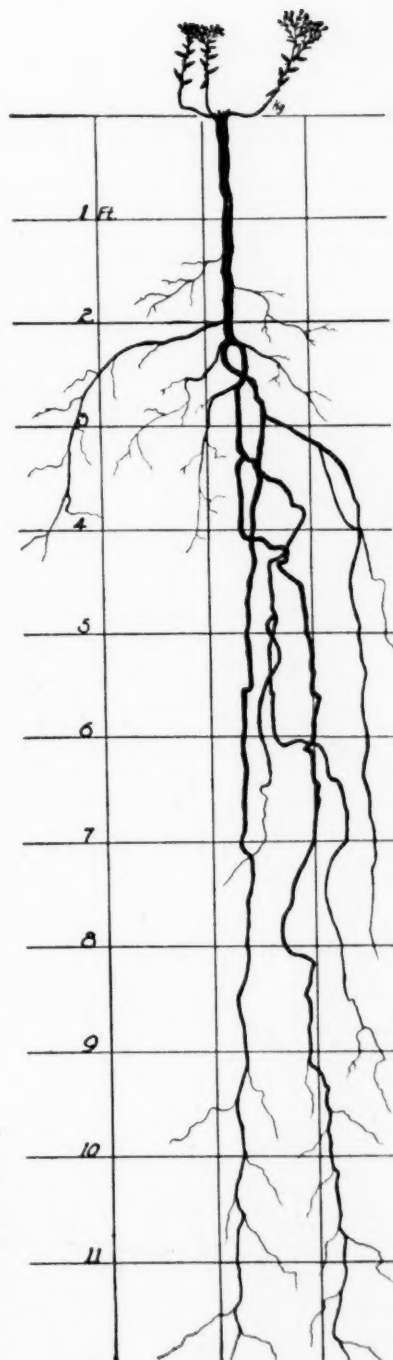


FIG. 23. Tap root and top of *Kuhnia glutinosa* excavated after the great drought of 1934, which had reduced the number of stems.

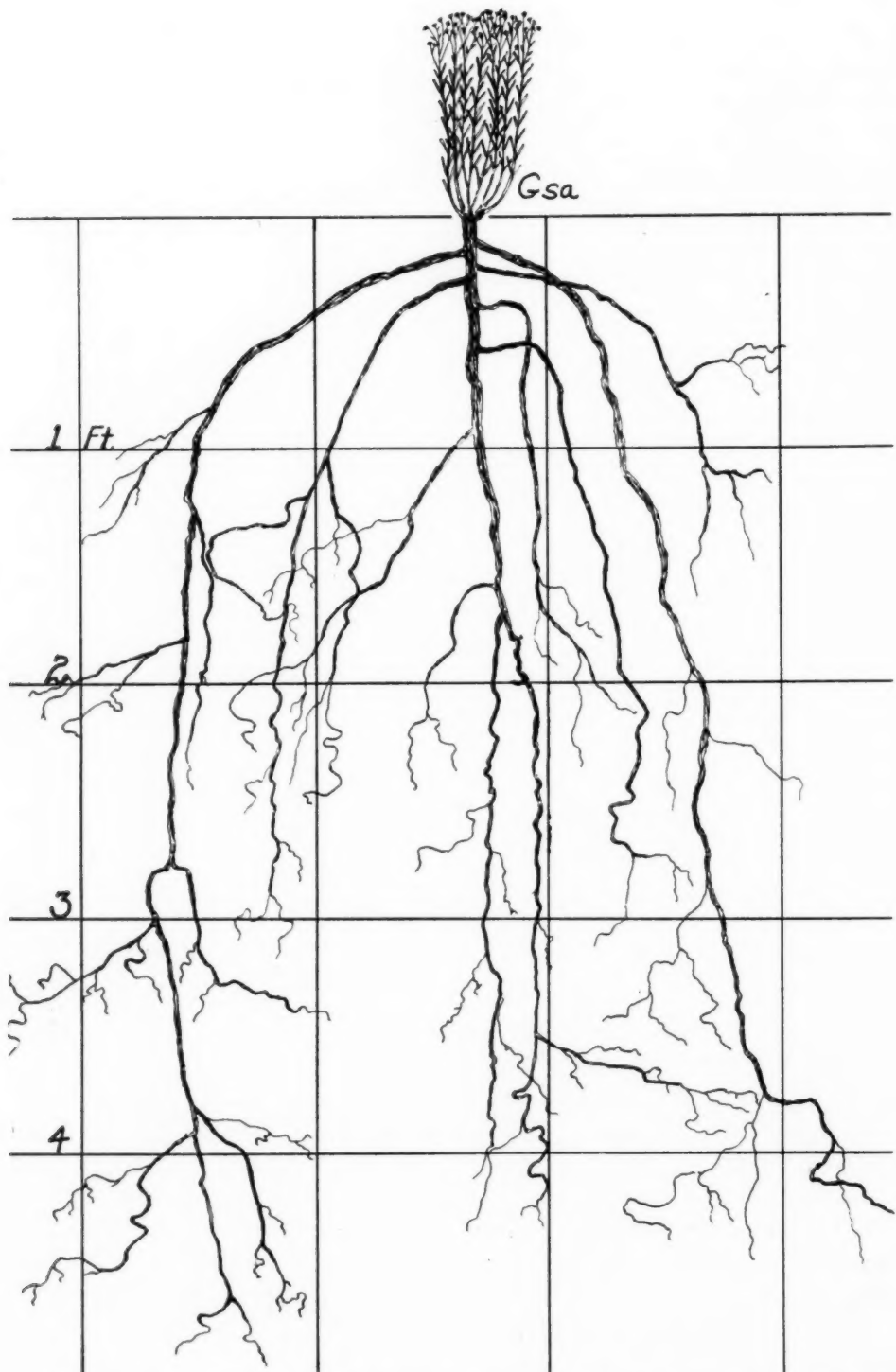


FIG. 24. The broom weed (*Gutierrezia sarothrae*), showing the great extent of roots in relation to top.

cieties are mostly rather definitely delimited. The tap root may extend to a depth of 6 feet. Many relatively fine laterals, however, occupy the surface 24 inches (Fig. 25).

The short-grass community is characterized further by a group of forbs which make a vigorous early growth and usually blossom before they are overtaken by summer drought. The most prominent are *Thelesperma gracile*, *Petalostemum purpureum*, *Ratibida columnaris* and *Sideranthus spinulosus* (Fig. 26). *Allionia linearis*, *Lygodesmia juncea*, *Gaura coccinea* and *Stenosiphon linifolium* are likewise chief members of this group (Fig. 27). Most of these plants usually have tap roots that extend to a depth of only 2 to 3 feet. Those of *Allionia linearis* and *Lygodesmia juncea*, however, are usually 4 to 5 feet deep. The roots of *Stenosiphon linifolium* are fibrous and only slightly larger than the more coarsely rooted grasses.

A study was also made of the root relations of plants in the shallow depressions where percolation was found to be very slow. The plant cover in a belt transect 8 feet wide and 240 feet long was first charted. This included numerous typical shallow depressions. A geotome was driven into the

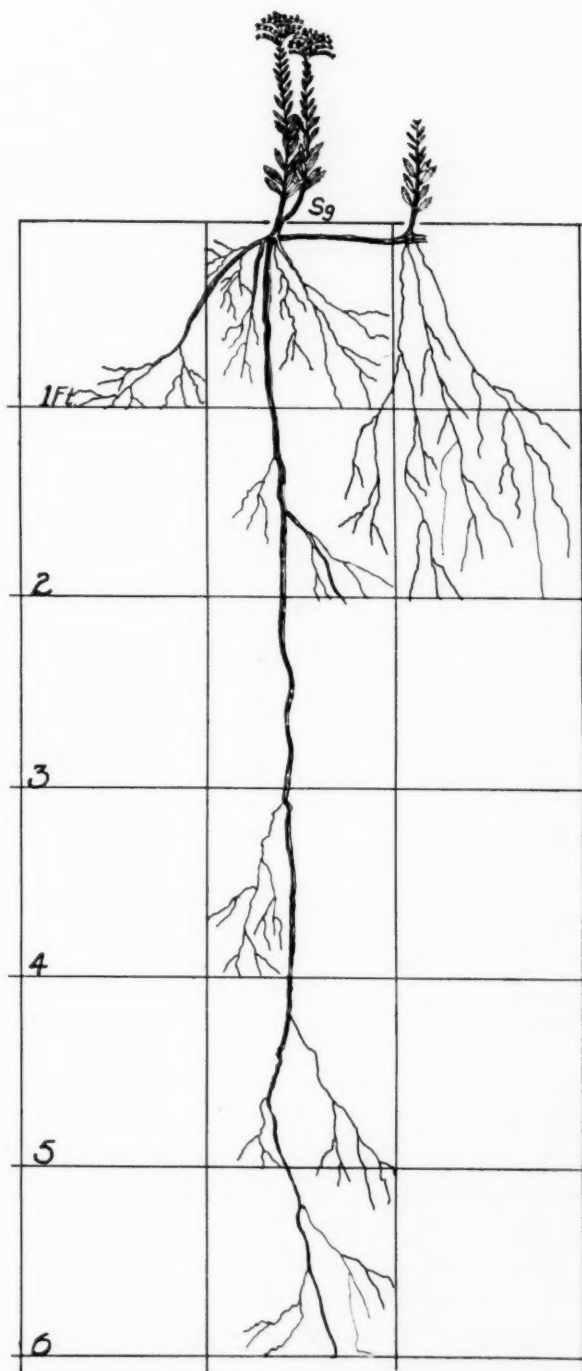


FIG. 25. Roots, rhizomes, and tops of *Solidago glaberrima*.

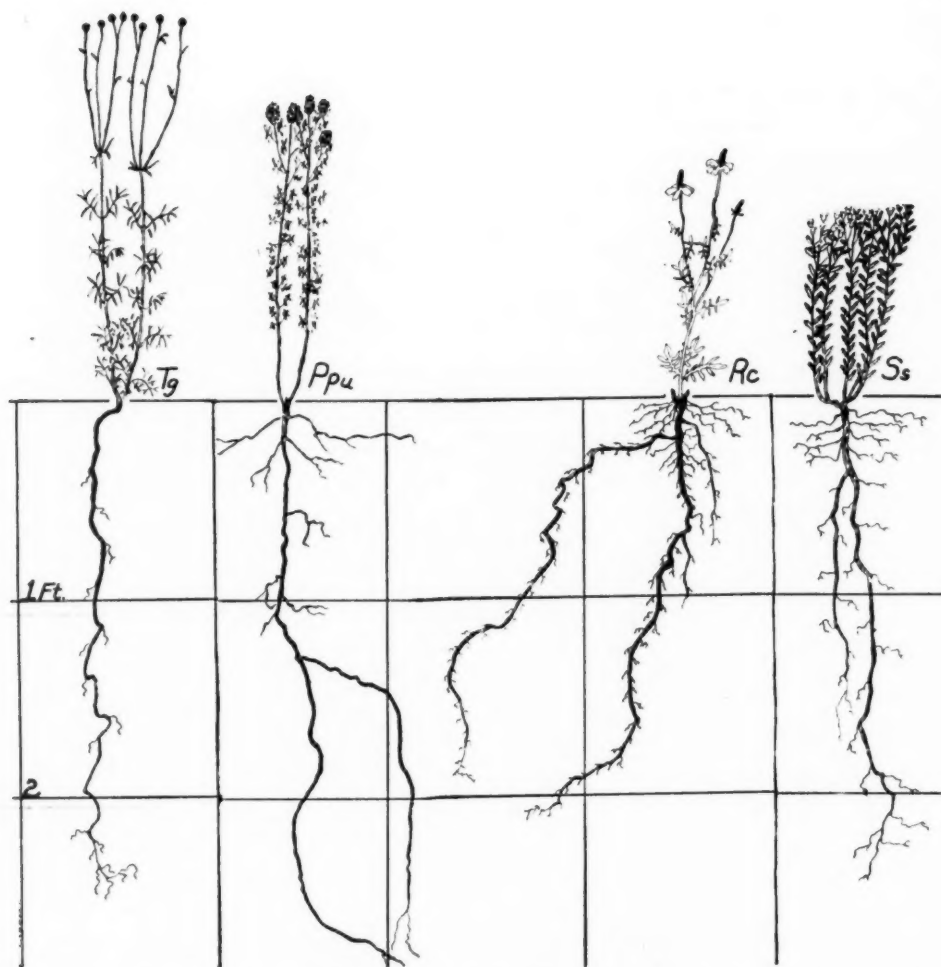


FIG. 26. A group of shallowly rooted forbs characteristic of the short-grass community. *Thelesperma gracile* (Tg); *Petalostemum purpureum* (Ppu); *Ratibida columnaris* (Rc); and *Sideranthus spinulosus* (Ss).

soil at 4-foot intervals throughout the length of the transect to determine its nature and the depth of the underlying rock. A portion of this is shown in Figure 28. The soil, thus removed, was carefully examined and the depth noted at which different soil layers were encountered. A profile was then constructed, but only after the examination of similar profiles of shorter lengths in other depressions.

The roots of the grasses in the shallow depressions seldom penetrated deeper than 12 inches while those of some of the forbs extended into the limestone beneath the layer of almost impervious soil.

ANDROPOGON SCOPARIUS TYPE

The habitat dominated by *Andropogon scoparius* is one of more favorable water relations compared with that of the short grasses. Little bluestem

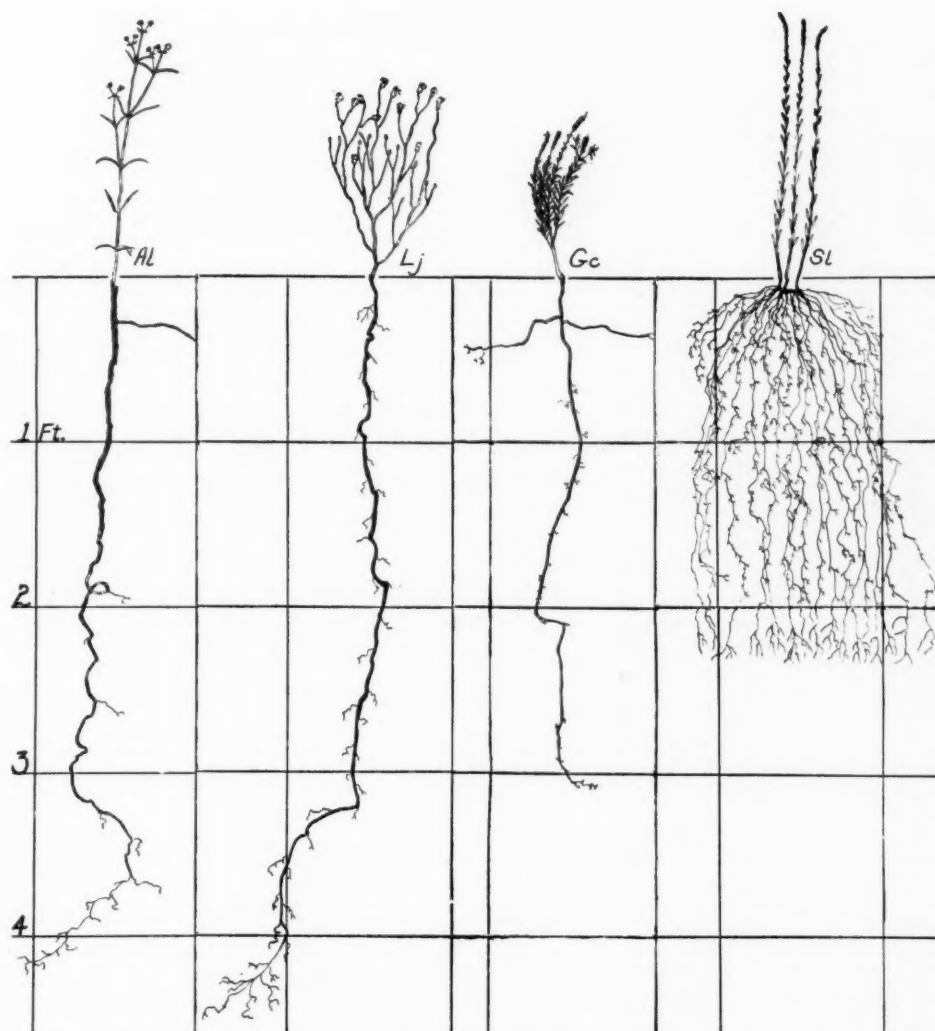


FIG. 27. Four species of forbs widely distributed among the short grasses. Note the meager branching of the tap roots of *Allionia linearis* (Al), *Lygodesmia juncea* (Lj), *Guara coccinea* (Gc), and the shallow but fibrous nature of the roots of *Stenosiphon linifolium* (Sl).

forms distinct bunches in drier places but a nearly continuous sod-mat in wetter ones. The landscape here appears light green in spring and early summer but reddish brown as the grass matures or is overtaken by drought. The dried grasses retain this reddish color throughout fall and winter. The usual height of the foliage, which is only slightly exceeded by the flower stalks, is 12 to 16 inches when mature, except during years of drought. Then it may not exceed 3 to 5 inches, and no flower stalks are produced. The bunches are usually 4 to 10 inches in diameter and spaced a distance equal at least to the width of the bunch. In the sod-mat type, however, they are much smaller and may be so numerous as to form a nearly continuous sod. Even when the bunches are 10 to 12 inches apart, this species is controlling.

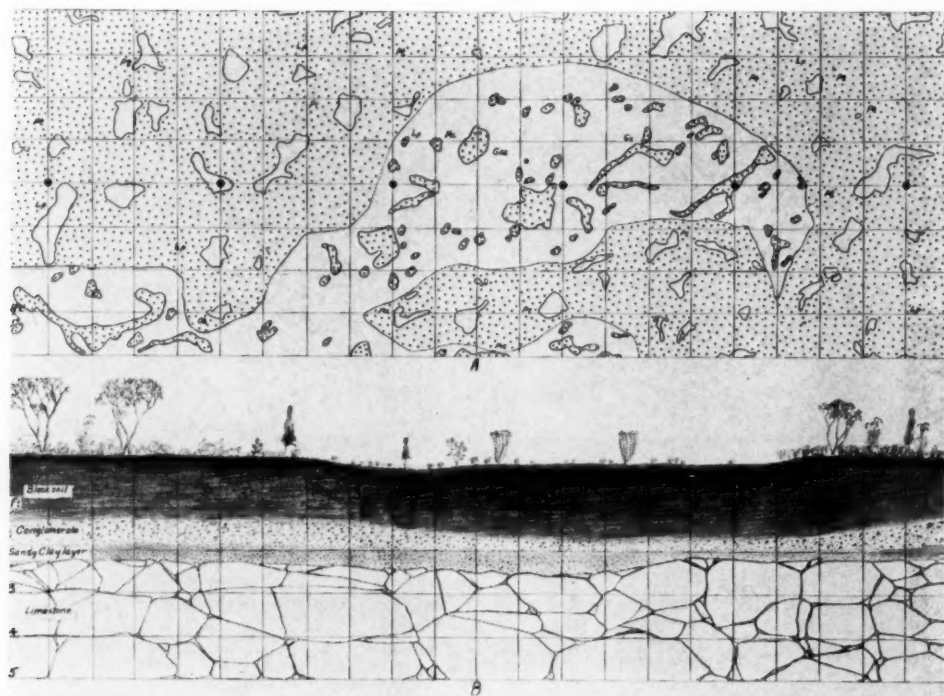


FIG. 28. (A) Belt transect showing heavy mat of short grass near a shallow depression and the thin cover of vegetation in it. (B) Profile showing soil layers penetrated by driving a geotome into the soil at 4-foot intervals (black dots) through the transect.

Scattered plants or clumps of *Andropogon furcatus*, 18 to 20 inches tall, overtop the dominant, and are sometimes so abundant as to furnish considerable competition. Isolated plants or small bunches of *Panicum virgatum* and *Sorghastrum nutans*, of similar height, also occur scattered throughout, and, even more frequently, the open bunches of *Bouteloua curtipendula*.

Closer examination shows that *Bouteloua hirsuta* and, less often, *Bouteloua gracilis* form tufts or small bunches. *Bulbilis dactyloides* is seldom present. *Sporobolus pilosus*, a dropseed only 8 inches in height, occurs in distinct bunches 3 to 6 inches in diameter. In general the lower layer of short grass is very meager. Hence, mixed prairie with a well developed understory is found over the broad ecotone above the brows of the hills. Here over moderately sloping ground little bluestem is endeavoring to gain possession of terrain held tenaciously by the short grasses. Here it is that a wave of tall grasses moves outward during periods of good precipitation only to retreat when continued drought is severe.

Various societies of forbs are conspicuous throughout the year, since this type has more species and better developed societies than either of the others. Water is more plentiful here than in the short-grass sod and shade is less dense than under cover of the big-bluestem type of the lower

ground. Numerous societies such as those of *Malvastrum coccineum*, *Anemone caroliniana* and *Allium nuttallii* do not occur; others not found in the area of short grasses, especially *Amorpha canescens*, *Echinacea pallida* and *Tetraneuris stenophylla*, are here well developed. Here too is found the most abundant growth of *Psoralea tenuiflora*. *Viorna fremontii*, *Lacinaria punctata*, *Tithymalus arkansanus*, *Cheirinia aspera*, *Meriolix serrulata* and *Spermolepis patens* are other species characteristic of this habitat.

Three well-developed layers occur above ground. *Bouteloua hirsuta*, *Bouteloua gracilis* and various low herbs such as *Paronychia jamesii* and *Scutellaria resinosa* characterize the first. Little bluestem, slender grama and the dropseed form the middle layer, which is best developed. Plants of greater height extend above this level. These include big bluestem, tall panic grass, *Amorpha canescens*, *Echinacea pallida*, *Psoralea tenuiflora* and *Ambrosia psilostachya*. Other species are *Parosela enneandra*, *Stenosiphon linifolium*, *Gaura parviflora* and *Yucca glauca*.

Layering below ground is also marked. In general the forbs that bloom in spring or early summer are rooted shallowly, extending only about 2 feet deep. The grasses form a well defined layer, extending to about the 3-foot level on south-facing slopes where the soil is shallower and to about 4 feet on north slopes. Below these the deeply rooted forbs extend downwards 4 to 6 feet on south slopes but 6 to 12 on the well-protected, north-facing ones.

The north slopes are protected from the prevailing winds and excessive isolation, and receive much water from wind-drifted snow. A few woody species are able to grow in the best protected places. Chief among the low-growing, woody plants are *Ceanothus ovatus*, *Prunus besseyi*, *P. melanocarpa*, *Rhus glabra*, *R. trilobata*, *Ribes odoratum*, *Symphoricarpos vulgaris*, *S. racemosus* and *Vitis vulpina*. Small trees of *Ulmus americana* and *Celtis occidentalis* occur infrequently.

The basal cover in the little-bluestem type is usually 40 to 60 per cent under average conditions of development. The normal foliage cover varies from 80 to 100 per cent. The cover varied considerably during the years of this study. In one permanent quadrat, for example, the basal cover of little bluestem was 53 per cent and that of slender grama grass about 1 per cent in 1932 (Fig. 29). Great losses had occurred by the fall of 1935. The total basal cover was reduced to 33 per cent. Little bluestem had been reduced to only 10 per cent, but slender grama grass had increased to 13. This increase of the more xeric slender grama grass following the death of little bluestem was a widespread phenomenon, notwithstanding the fact that many of the older and larger bunches of the grama grass died.

Big bluestem, where it occurred with the smaller dominant, often withstood extreme drought and even increased its area while little bluestem succumbed more or less completely. A typical case is shown in Figure 30. In 1932 the basal cover of the smaller grass was 55.6 per cent, but it was

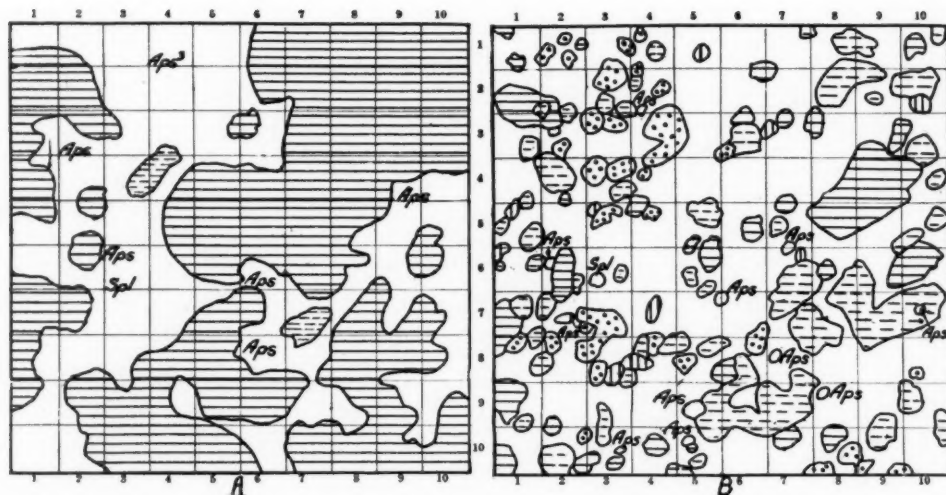


FIG. 29. (A) Meter quadrat showing sod-mat type of little bluestem in 1932. (B) Same after 3 years of drought. Little bluestem (horizontal hatch); slender grama grass (broken horizontal hatch); blue grama grass (stippled); *Ambrosia psilostachya* (Aps); and *Senecio plattensis* (Spl).

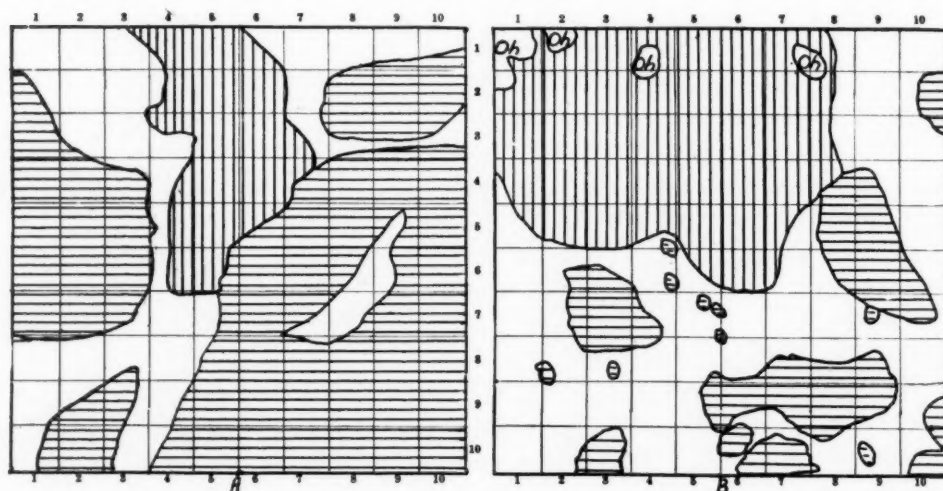


FIG. 30 (A) Meter quadrat in 1932 showing a typical area where big bluestem (perpendicular hatch) is mixed with little bluestem (horizontal hatch). (B) Same area after drought of 1934. Slender grama grass (broken horizontal hatch) and *Opuntia humifusa* (Oh) have invaded the area.

only 17 per cent in the fall of 1934. The more deeply rooted big bluestem, however, increased its area from 13 to 33 per cent during the same period.

The sparse plant cover on the brows of the hills is shown in Figure 31. Here little bluestem covered 30 per cent of the soil in 1932 but was reduced to 23 per cent by the fall of 1935.

Little bluestem is also often found in scattered bunches among the short grasses where the slope is gentle. Where the descent is abrupt, however,

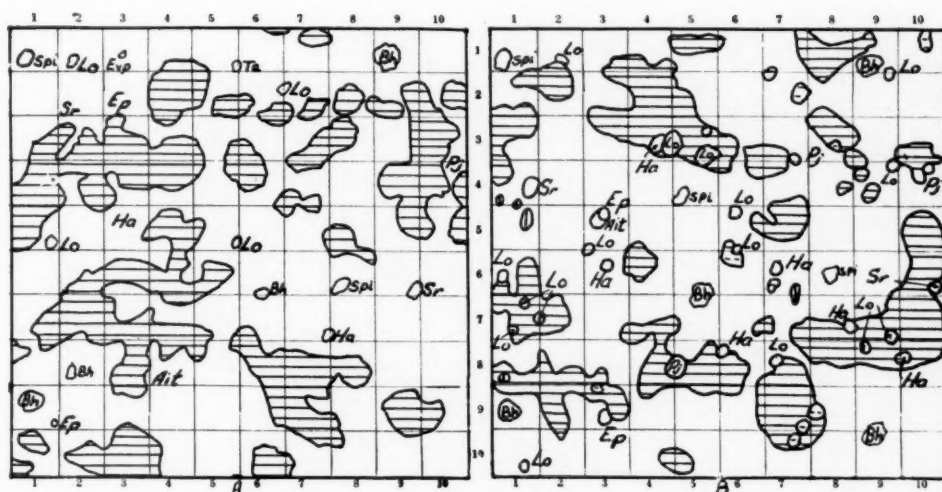


FIG. 31. Meter quadrat of typical bunch-type of little bluestem on brows of hills: (A) Charted in the fall of 1932 and (B) in fall of 1935. *Sporobolus pilosus* (Spi); *Lesquerella ovalifolia* (Lo); *Evolvulus pilosus* (Evp); *Tetraeneuris stenophylla* (Ta); *Bouteloua hirsuta* (Bh); *Houstonia angustifolia* (Ha); *Arenaria texana* (Ait); *Echinacea pallida* (Ep); *Scutellaria resinosa* (Sr); and *Paronychia jamesii* (Pj).

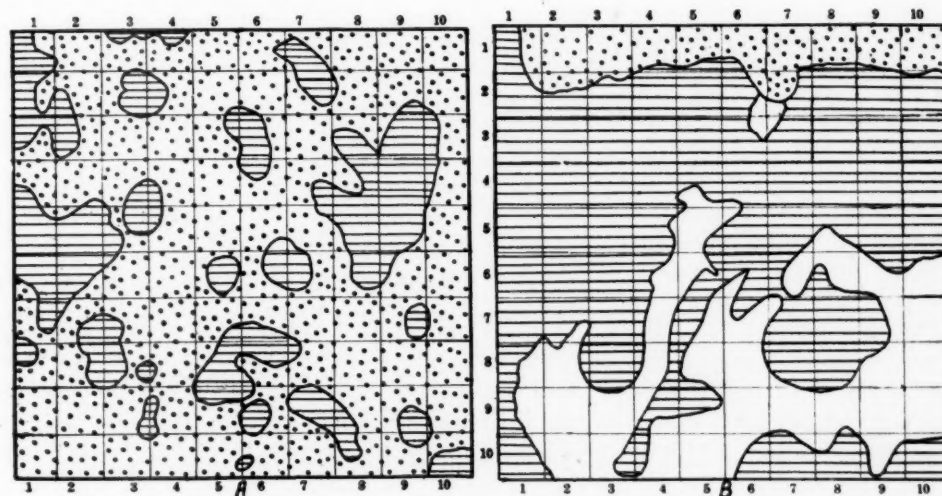


FIG. 32. (A) Typical meter quadrat on gentle slope where short grasses (stippled) form an understory to the scattered bunches of little bluestem (horizontal hatch). (B) Quadrat on an abrupt slope where the two types are separated by a sharp line. Both were charted in the fall of 1932.

relatively pure stands of each type lie in close juxtaposition. Both of these conditions are illustrated in Figure 32.

Two quadrats from opposite lower slopes often reveal distinctly different kinds of vegetation. One from the south-facing slope, where the impervious blue clay supported short grasses, and another from the same height on the north hillside, where the tall, dense growth of the big bluestem grasses is well developed, are shown in Figure 33. The forbs are also different. The

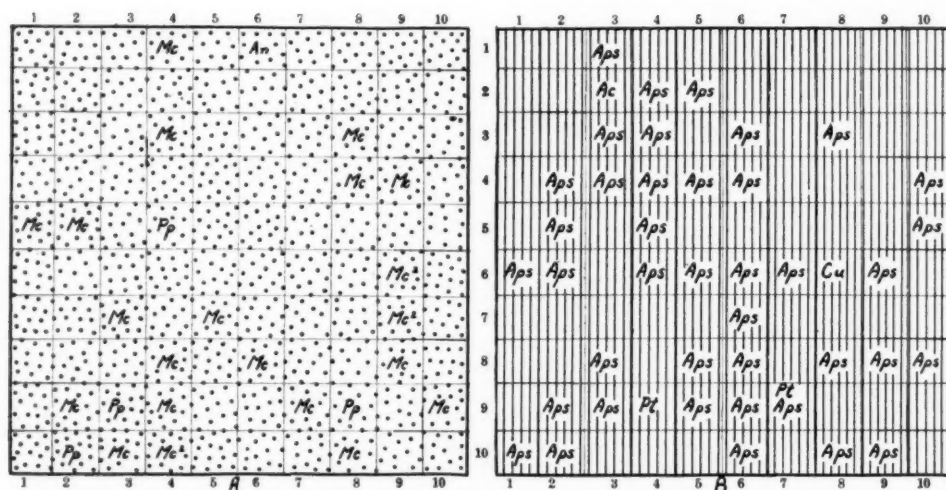


FIG. 33. Meter quadrats on opposite lower slopes: (A) South-facing slope occupied by short grasses (stippled); (B) North-facing slope occupied by big bluestem (perpendicular hatch). *Malvastrum coccineum* (Mc), *Allium nuttallii* (An) and *Plantago purshii* (Pp) are common among the short grasses. *Ambrosia psilostachya* (Aps), *Amorpha canescens* (Ac), *Cirsium undulatum* (Cu) and *Psoralea tenuiflora* (Pt) are associated with big bluestem.

drought resistant *Malvastrum coccineum* and *Plantago purshii* are associated with the short grasses, and *Ambrosia psilostachya*, *Amorpha canescens* and *Psoralea tenuiflora* with the taller, less xeric bluestem.

The bluestems renew growth early in April, almost a month later than the short grasses. Little bluestem reaches its maximum development of foliage in July, flowers in August and September, and dies only with the coming of severe frost. Growth may cease, however, during periods of intense drought. Early in June the foliage of big bluestem extends to a height of 4 to 12 inches. It reaches a maximum height of 18 to 24 inches in August and September if soil moisture is plentiful. If the weather is extremely dry, however, foliage is dwarfed and flower stalks fail to develop.

The grasses and forbs of the little-bluestem community are grouped according to their ecological importance in Table 7. A few rare species are not included.

TABLE 7. PLANTS OF THE LITTLE-BLUESTEM HABITAT

Dominant species

Andropogon scoparius Michx.

Principal species of grasses

Andropogon furcatus Muhl.

Bouteloua curtipendula (Michx.) Torr.

Bouteloua gracilis (H. B. K.) Lag.

Bouteloua hirsuta Lag.

Panicum virgatum L.

Sitanion elymoides Raf.

Sorghastrum nutans (L.) Nash
Sporobolus pilosus Vasey

Grasses of secondary importance

Bulbilis dactyloides Raf.
Eatonia obtusata A. Gray
Festuca octoflora Walt.
Koeleria cristata (L.) Pers.
Sporobolus asper (Michx.) Kunth
Sporobolus cryptandrus (Torr.) A. Gray
Triodia acuminata Vasey

Principal species of forbs

Ambrosia psilostachya DC.
Amorpha canescens Pursh
Echinacea pallida (Nutt.) Britton
Lacinaria punctata (Hook.) Kuntze
Meriopsis serrulata (Nutt.) Walp.
Psoralea tenuiflora Pursh
Tetrameuris stenophylla Rydb.

Forbs of secondary importance

Acerates auriculata Engelm.
Acerates viridiflora (Raf.) Eaton
Acuan illinoensis (Michx.) Kuntze
Allionia linearis Pursh
Aster multiflorus Ait.
Aster oblongifolius Nutt.
Astragalus missouriensis Nutt.
Astragalus mollissimus Torr.
Astragalus shortianus Nutt.
Castilleja sessiliflora Pursh
Cheirinia aspera (Nutt.) Rydb.
Cirsium undulatum (Nutt.) Spreng.
Croton monanthogynus Michx.
Croton texensis (Klotzsch) Muell. Arg.
Erigeron ramosus (Walt.) B. S. P.
Euphorbia dentata Michx.
Galpinsia lavendulaefolia (T. & G.) Small
Guara coccinea Nutt.
Gaura parviflora Dougl.
Glycyrrhiza lepidota Nutt.
Grindelia squarrosa (Pursh) Dunal
Gutierrezia sarothrae (Pursh) Britton and Rusby
Hedeoma hispida Pursh
Hedeoma longiflora Rydb.
Helianthus maximiliani Schrad.
Hymenopappus corymbosus T. and G.
Leucelene ericoides (Torr.) Greene
Linum compactum A. Nels.
Linum sulcatum Riddell
Lithospermum linearifolium Goldie
Lygodesmia juncea (Pursh) D. Don.

Malvastrum coccineum (Nutt.) A. Gray
Morongia uncinata Britton
Nuttallia decapetala (Pursh) Greene
Onosmodium occidentale Mackenzie
Oxalis stricta L.
Oxytropis lambertii Pursh
Parosela aurea (Nutt.) Britton
Parosela enneandra (Nutt.) Britton
Pentstemon albidus Nutt.
Petalostemum oligophyllum Torr.
Petalostemum purpureum (Vent.) Rydb.
Physalis comata Rydb.
Polygala alba Nutt.
Psoralea argophylla Pursh
Psoralea cuspidata Pursh
Psoralea esculenta Pursh
Ratibida columnaris (Sims.) D. Don.
Rosa pratincola Greene
Senecio plattensis Nutt.
Sideranthus spinulosus (Pursh) Sweet
Silphium integrifolium Michx.
Silphium laciniatum L.
Sophora sericea Nutt.
Specularia leptocarpa (Nutt.) A. Gray
Specularia perfoliata (L.) A. DC.
Spermolepis patens (Nutt.) Robinson
Solidago glaberrima Martens
Solidago mollis Bartl.
Solidago rigida L.
Stenosiphon linifolium (Nutt.) Britton
Thelesperma gracile (Torr.) A. Gray
Tithymalus arkansanus (Engelm. and Gray) Kl. and Grache
Townsendia exscapa (Richards) Porter
Verbena bracteosa Michx.
Viorna fremontii (S. Wats.) Heller

Forbs found only on brows of hills

Arenaria texana Britton
Comandra pallida A. DC.
Evolvulus pilosus Nutt.
Houstonia angustifolia Michx.
Lesquerella ovalifolia Rydb.
Megapterium fremontii (S. Wats.) Britton
Mentzelia oligosperma Nutt.
Parietaria pennsylvanica Muhl.
Paronychia jamesii T. & G.
Scutellaria resinosa Torr.
Tragia ramosa Torr.

UNDERGROUND PARTS IN RELATION TO TOPS

In determining the ecological relationships of the species underground, pick axes and iron bars with sharp ends were used to loosen the limestone

layers. By this means only was it possible to examine the rock crevices and soil through which the roots penetrated. Vegetation characteristic of the south-facing slopes is shown in Figure 34. The roots of little bluestem and slender grama, though relatively fine, penetrate only to about 3 feet. Those

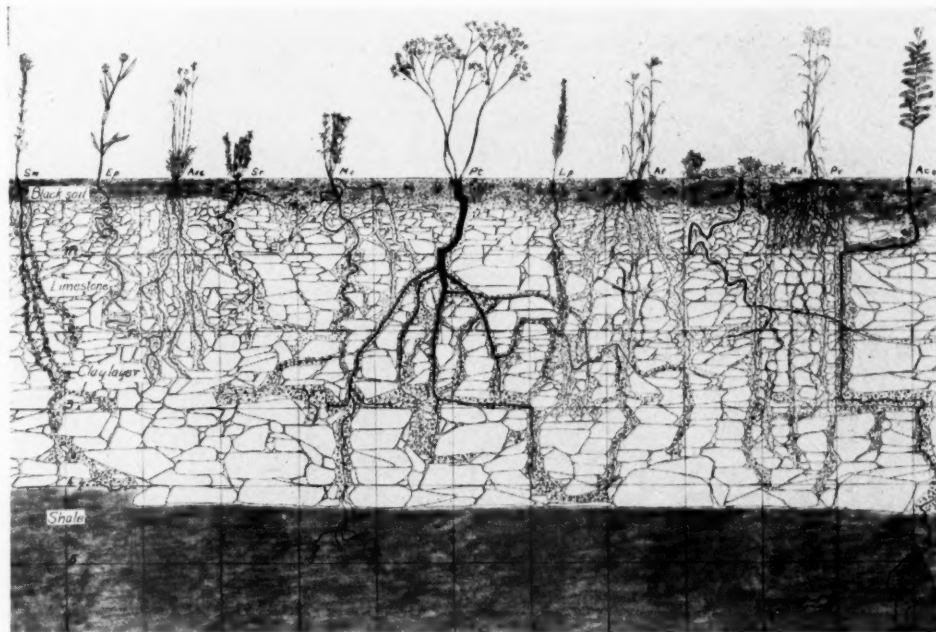


FIG. 34. Bisect showing relations of roots and tops of grasses and forbs on a typical south-facing slope where the soil is shallow. *Solidago mollis* (Sm); *Echinacea pallida* (Ep); *Andropogon scoparius* (Asc); *Scutellaria resinosa* (Sr); *Meriolix serrulata* (Ms); *Psoralea tenuiflora* (Pt); *Lacinaria punctata* (Lp); *Andropogon furcatus* (Af); *Morongia uncinata* (Mu); *Panicum virgatum* (Pv) and *Amorpha canescens* (Ac).

of the big bluestem, tall panic grass and Indian grass usually extend 1 to 2 feet deeper. The fine roots of hairy grama grass, blue grama grass and buffalo grass are usually confined to the surface 18 inches.

Amorpha canescens is the most important forb in this habitat. It overtops the dominant grasses and lends a silvery gray cast to the landscape. The tap root, often somewhat branched, may extend to a depth of 6 to 9 feet through the clay layers.

Psoralea tenuiflora also is usually abundant on the slopes. It begins growth about May 1 and reaches its maximum height of 18 to 24 inches during late June. The root system of the plant is usually modified by the underlying limestone layers. It is often much branched where relatively solid layers of rock are encountered; otherwise the tap root is poorly divided and penetrates to a depth of 7 to 9 feet.

Lacinaria punctata, *Echinacea pallida*, *Meriolix serrulata* and *Morongia uncinata* are all widely scattered forbs of considerable importance. The first

species blossoms in late summer; the others reach their maximum anthesis about the middle of June. None have roots that extend deeper than 3 feet (Fig. 34).

Some of the plants commonly found on the well protected, north-facing slopes are shown in Figure 35. The roots of the dominant grasses penetrate

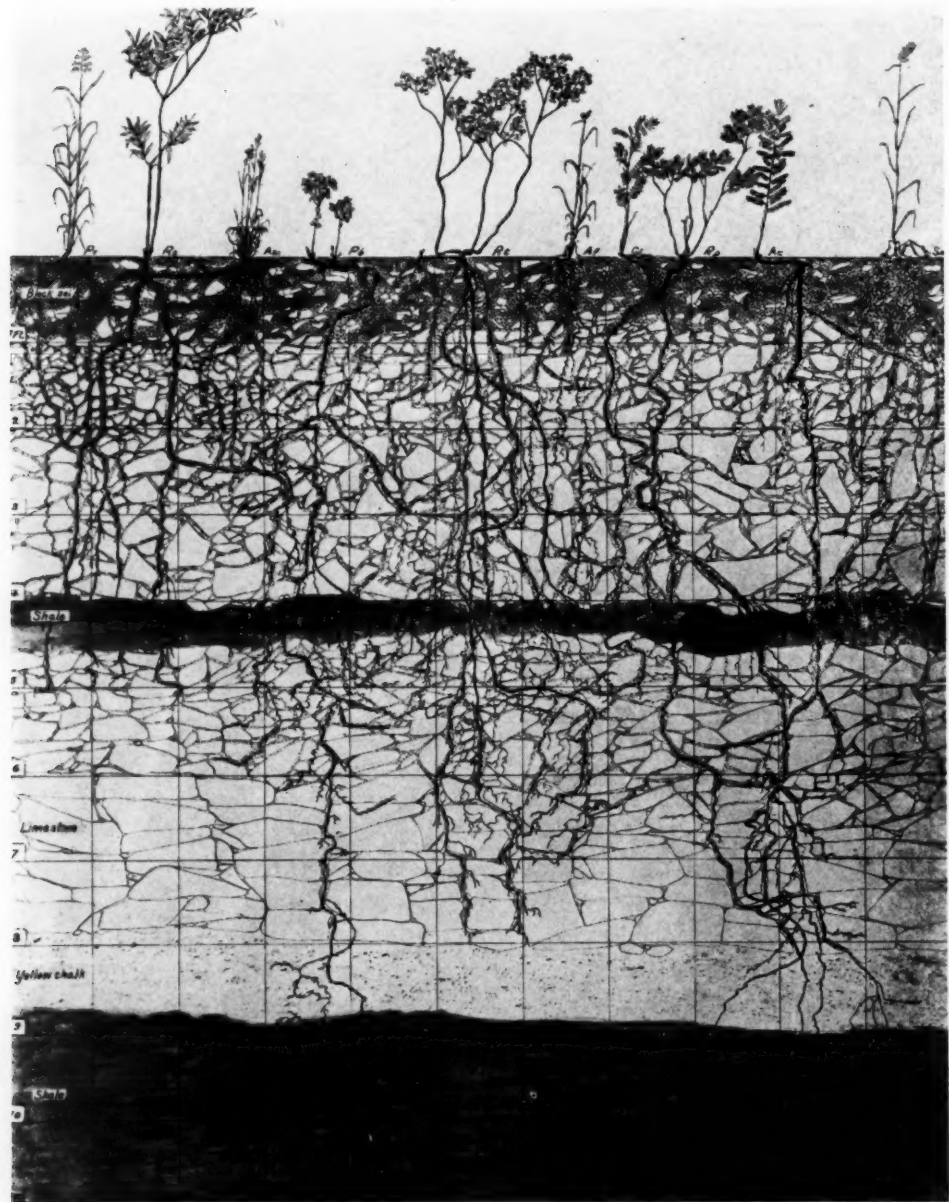


FIG. 35. Bisect showing soil and relations of roots and tops of plants on a well protected north-facing slope. *Panicum virgatum* (Pv); *Rhus glabra* (Rg); *Andropogon scoparius* (Asc); *Prunus besseyi* (Pb); *Rhus trilobata* (Rt); *Andropogon furcatus* (Af); *Glycyrrhiza lepidota* (Gl); *Rosa pratincola* (Rp); *Amorpha canescens* (Ac) and *Sorghastrum nutans* (Sn).

slightly deeper than those in the drier locations. The fibrous roots of little bluestem are often found at a depth of 4 feet or more but the coarser roots of big bluestem, tall panic grass, and Indian grass frequently penetrate considerably deeper.

The coarse roots of *Rhus glabra* grow from heavy rhizomes and extend to a depth of 5 feet or more. Those of *R. trilobata* are commonly coarse, much branched, and reach depths of at least 8 feet. *Prunus besseyi*, though small in stature above ground, has a prominent tap root that often terminates in many small branches at a depth of 11 feet. The tortuous roots of *Glycyrrhiza lepidota* and *Rosa pratincola* are also very extensive. After considerable diversity in direction of growth, they finally terminate in the shale at a depth of 10 to 12 feet.

Asclepiodora decumbens is usually found along the slopes where the soil is moderately deep (Fig. 36). The thick, woody root has many laterals that run in a nearly horizontal direction.

Viorna fremontii is commonly limited to the upper slopes above the brows of the hills. The unbranched, fleshy roots spread widely and extend to a depth of about 2 feet (Fig. 36).

The little-bluestem habitat is further characterized by a group of small, early-blooming plants that are usually limited to the brows of the hills. Important among these are *Senecio plattensis*, *Ditaxis mecurialina*, *Arenaria texana*, *Leucelene ericoides*, *Houstonia angustifolia* and *Scutellaria resinosa* (Fig. 37). Associating with these and of equal rank are *Megapterium fremontii*, *Lithospermum linearifolium*, *Lesquerella ovalifolia*, *Paronychia jamesii* and *Evolvulus pilosus* (Fig. 38).

ANDROPOGON FURCATUS TYPE

The lower slopes and ravines where water content of soil is most favorable are dominated by big bluestem and its associates. Where fall mowing or fire has removed the debris, the appearance in spring is that of a luxuriant

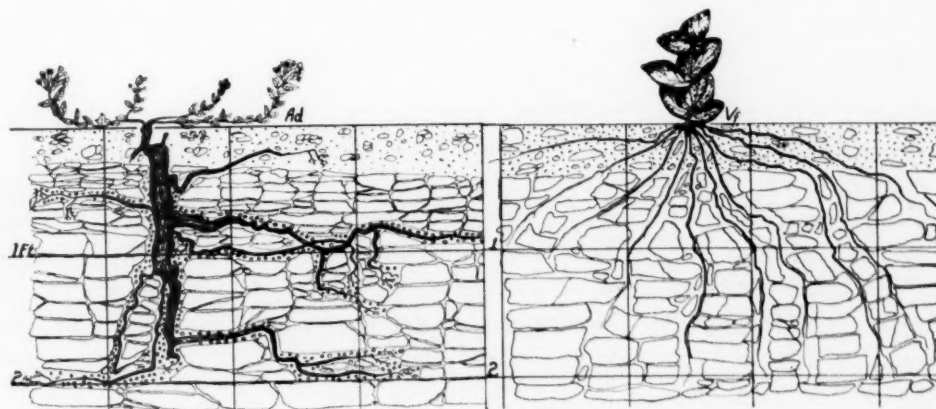


FIG. 36. Two common forbs of the little-bluestem type. *Asclepiodora decumbens* (Ad) and *Viorna fremontii* (Vf).

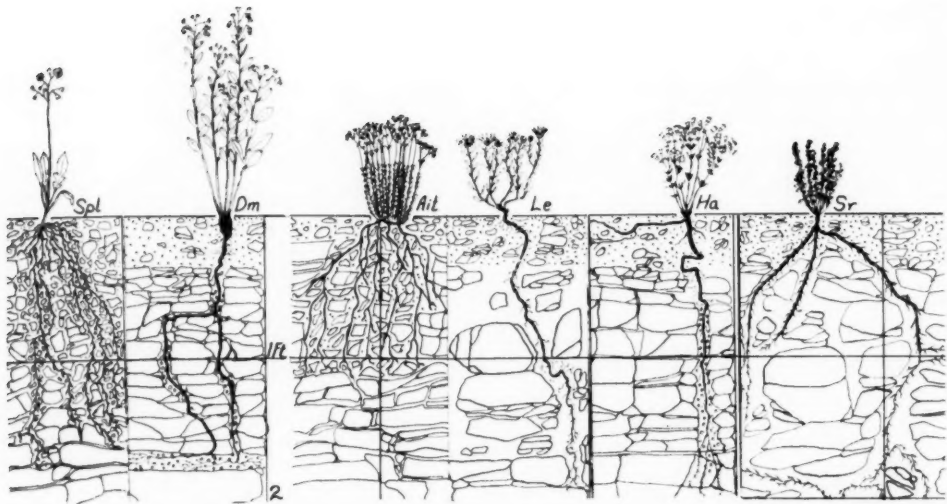


FIG. 37. Group of shallowly rooted forbs found near the brows of the hills. *Senecio plattensis* (Spl); *Ditaxis mecurialina* (Dm); *Arenaria texana* (Ait); *Leucelene ericoides* (Le); *Houstonia angustifolia* (Ha) and *Scutellaria resinosa* (Sr).

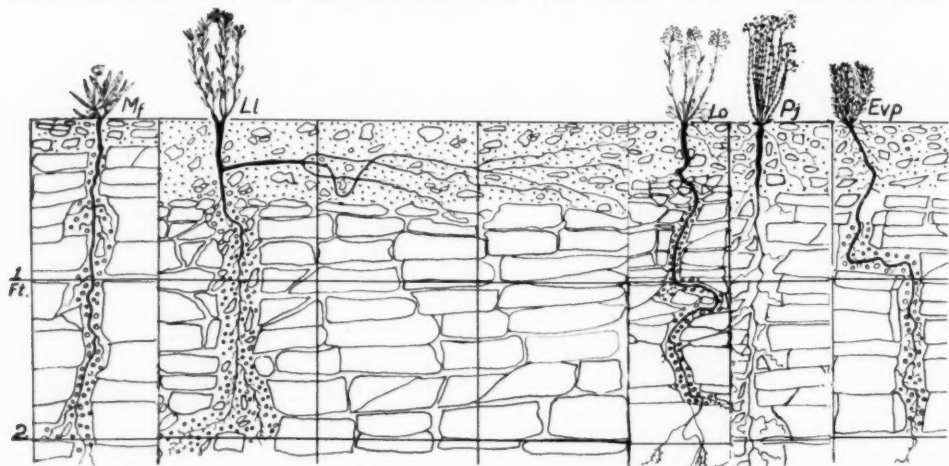


FIG. 38. Shallowly rooted forbs found on the brows of the hills where the soil is thin. *Megapterium fremontii* (Mf); *Lithospermum linearifolium* (Ll); *Lesquerella ovalifolia* (Lo); *Paronychia jamesii* (Pj) and *Evolvulus pilosus* (Evp).

meadow. The numerous perennial, sod-forming grasses and mostly coarse forbs resume growth early. Development is rapid, despite the long season for growth. In early June the waving foliage is 8 inches tall and by late July growth is almost complete. The general level is 20 inches if the year is one of good rainfall. Estival and autumnal forbs compete with the grasses for light and often overtop them even after the height of the grasses has been somewhat increased by the development of flower stalks. It is here, as on the hillsides covered with bunch grasses, that the brilliant autumnal colors are so pronounced.

Andropogon furcatus alone usually composes about 75 per cent of the vegetation. Its chief associates are *Bouteloua curtipendula*, *Agropyron smithii*

and *Sporobolus drummondii*. *Panicum virgatum*, *Sorghastrum nutans*, *Elymus canadensis*, *E. virginicus* and *Carex graxida*, although occurring in a mixture with the dominants, are more abundant in somewhat wetter situations. *Poa arida* forms a rather light understory throughout. Often the normal distribution is interrupted on slight elevations by island-like areas where *Bouteloua gracilis* is poorly concealed by a thin stand of big bluestem or other tall grasses.

It was not feasible to use a pantograph in determining basal cover of these tall grasses. Hence the plants were listed and the ground cover in each square decimeter accurately estimated. Twelve meter quadrats in several widely separated but typical ravines were studied (Fig. 39). The basal cover per square decimeter frequently ranged from 2 to 25 per cent in a single square-meter area. The average for the 12 quadrats was 11.2 per cent.

The percentage of the 1,200 square decimeters in which each species occurred is shown in Table 8. The consistent presence of big bluestem (93 per cent) helps to explain its dominance. Slender grama grass, with 34 per cent, ranks second. It has increased considerably at the expense of big bluestem during the drought as have also western wheat grass and the blue grama grass.

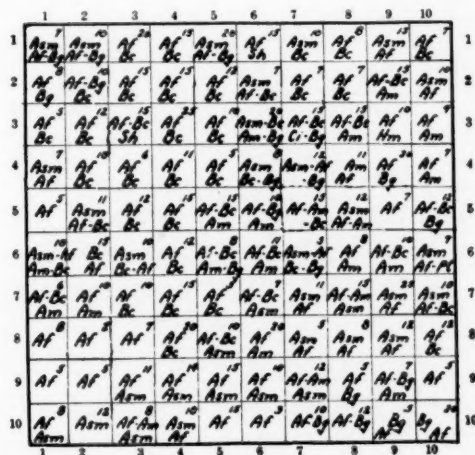


FIG. 39. Representative meter quadrat in the big-bluestem consociation showing the percentage of basal cover in each square decimeter and the species composing it. Symbols as in Table 8.

TABLE 8. Percentage distribution of grasses and forbs in 12 square meters in the big-bluestem consocieties. Species found in less than 1 per cent of the unit areas are not recorded.

Species	Symbol	Per cent
<i>Andropogon furcatus</i>	Af	93
<i>Bouteloua curtipendula</i>	Bc	34
<i>Agropyron smithii</i>	Asm	20
<i>Sporobolus drummondii</i>	Sh	18
<i>Panicum virgatum</i>	Pv	7
<i>Elymus virginicus</i>	Ev	6
<i>Aster multiflorus</i>	Am	5
<i>Bouteloua gracilis</i>	Bg	3
<i>Carex graxida</i>	Cg	3
<i>Psoralea tenuiflora</i>	Pt	3
<i>Callirrhoe involucrata</i>	Ci	2
<i>Salvia pitcheri</i>	Sp	2
<i>Sorghastrum nutans</i>	Sn	2

Big bluestem begins growth between April 15 and May 1 depending upon the season and the density of the dead foliage on the surface of the soil. By early July it reaches a height of 8 to 15 inches and 2 weeks later a heavy layer of foliage often extends to 20 inches. Flower stalks are then produced. They reach their maximum height of about 4 feet near the middle of August. As fall approaches the green color changes to reddish brown.

Western wheat grass and nodding wild rye are the earliest of all the grasses in this community. Early in March the lower slopes and drier places in the ravines are covered with a bluish-green cast characteristic of wheat grass. The foliage develops rapidly. Flower stalks begin to form by the middle of June and soon reach a maximum height of 24 to 36 inches. The nodding wild rye also blossoms by midsummer.

The narrow green shoots of slender grama grass begin growth early in April. A dense mat of foliage is soon formed near the surface of the soil. Flower stalks, supporting the long slender inflorescences, soon extend to a height of 16 to 24 inches above the foliage.

Sporobolus drummondii renews growth relatively late. Slender, narrow, basal leaves, 15 to 24 inches long, are common by July 1. Late in August many panicles are found partially enclosed in the upper sheaths.

Panicum virgatum is most abundant in the wetter situations. Dense bunches 2 to 6 feet in diameter are common. Growth is resumed late in April. The foliage reaches a height of about 20 inches early in July. Flower stalks soon appear and reach a maximum height of approximately 36 inches.

Sorghastrum nutans may occur as isolated plants but usually grows in distinct bunches where moisture relations are most favorable. Green shoots appear about May 1 and a month later a height of 12 inches is common. The golden-colored flower heads appear about the middle of August and maximum anthesis is reached a month later.

The lowland vegetation is characterized by a mixture of grasses and forbs of unusual stature, coarseness of stems, and high percentage of foliage cover, although 85 to 90 per cent of the soil surface is unoccupied.

Three more or less distinct layers occur. The grasses constitute the best developed middle one. Important forbs associated with the grasses in their principal story of vegetation are *Kuhnia glutinosa*, *Aster multiflorus*, *Amorpha canescens* and *Psoralea tenuiflora*. Various other forbs also occur at this level. *Salvia pitcheri*, *Vernonia baldwini*, *Helianthus maximiliani* and *Verbena stricta* are representative of species which overtop the grasses and constitute a poorly developed upper story. Chief among the plants of the lower story are *Callirhoe involucrata*, *Lippia cuneifolia*, *Vicia sparsifolia*, *Lythrum alatum* and *Viola papilionacea*. They mature comparatively early, completing their life cycle while light is still plentiful. *Poa arida* is an important grass of the understory.

The grasses and forbs of the big-bluestem community are arranged according to their ecological importance in Table 9. Some of the least important species are not included.

TABLE 9. PLANTS OF THE BIG-BLUESTEM HABITAT

Dominant species

Andropogon furcatus Muhl.
Agropyron smithii Rydb.
Bouteloua curtipendula (Michx.) Torr.
Sporobolus drummondii (Trin.) Vasey

Principal species of grasses and sedges

Andropogon torreyanus Steud.
Carex gravida Bailey
Elymus canadensis L.
Elymus virginicus L.
Panicum virgatum L.
Poa arida Vasey
Sorghastrum nutans (L.) Nash

Grasses of secondary importance

Bouteloua gracilis (H. B. K.) Lag.
Bulbilis dactyloides Raf.
Sporobolus asper (Michx.) Kunth
Sporobolus cryptandrus (Torr.) A. Gray

Principal species of forbs

Amorpha canescens Pursh
Aster multiflorus Ait.
Erigeron ramosus (Walt.) B. S. P.
Psoralea tenuiflora Pursh
Salvia pitcheri Torr.
Verbena stricta Vent.
Vernonia baldwini Torr.

Forbs of secondary importance

Acuan illinoensis (Michx.) Kuntze
Ambrosia psilostachya DC.
Asclepias pumila (A. Gray) Vail
Apocynum cannabinum L.
Callirrhoe involucrata (T. and G.) A. Gray
Cirsium undulatum (Nutt.) Spreng.
Euphorbia marginata Pursh
Gaura parviflora Dougl.
Glycyrrhiza lepidota Nutt.
Helianthus maximiliani Schrad.
Kuhnia glutinosa Ell.
Lippia cuneifolia (Torr.) Steud.
Lythrum alatum Pursh

Onosmodium occidentale Mackenzie
Ratibida columnaris (Sims.) D. Don.
Silphium integrifolium Michx.
Solidago glaberrima Martens
Solidago mollis Bartl.
Solidago rigida L.
Specularia leptocarpa (Nutt.) A. Gray
Specularia perfoliata (L.) A. DC.
Vicia sparsifolia Nutt.
Viola papilionacea Pursh

UNDERGROUND PARTS IN RELATION TO TOPS

Interrelations of the plants were studied not only above ground but also within the soil. The latter was accomplished by the usual trench system, roots and rhizomes being uncovered either by use of a pick or by washing the soil away with a spray of water (Fig. 40). The grass roots in this consocieties are usually coarse and, with the exception of *Elymus canadensis*, relatively deep.

Big bluestem has roots that grow from scaly rhizomes found in the surface 4 inches of the soil. They are tough and much branched. In areas where a dense sod is formed the upper 2 feet of soil is completely occupied by the roots of this species. Farther down, however, they gradually become less abundant and smaller but more finely branched. Comparatively few of the roots extend to a depth greater than 7 feet.

The xeric character of slender grama grass is indicated by its root system. The main roots, with many fine laterals, occupy the upper 3 feet of soil, and many roots extend to a depth of 6 to 7 feet.

The roots of western wheat grass are also finer than those of big bluestem. They grow from long, slender rhizomes, branch profusely, and reach a depth of approximately 7 feet. Those of *Elymus canadensis* are fine, have short branches, and extend downward approximately 2.5 feet.

Sorghastrum nutans and *Panicum virgatum* have coarse roots that develop from a dense mat of rhizomes. They completely occupy the upper 3 feet of soil and penetrate to about 8 feet. Those of *Carex grvida* branch profusely and extend downward to 6 feet.

The deep type of roots prevail in many of the important forbs such as *Kuhnia glutinosa*, *Amorpha canescens* and *Psoralea tenuiflora*. Here the depth of penetration varies from 8 to 11 feet. Roots of *Vernonia baldwini*, *Salvia pitcheri* and *Verbena stricta*, however, are thick, fleshy, and relatively shallow. Even the roots of *Aster multiflorus* are limited to the upper 4 to 6 feet.

DISCUSSION

The usual main distinctive feature of mixed prairie, which is the intimate mixing of tall and short grasses, is not pronounced at Hays. Over the general area of the association the short grasses regularly form a layer beneath

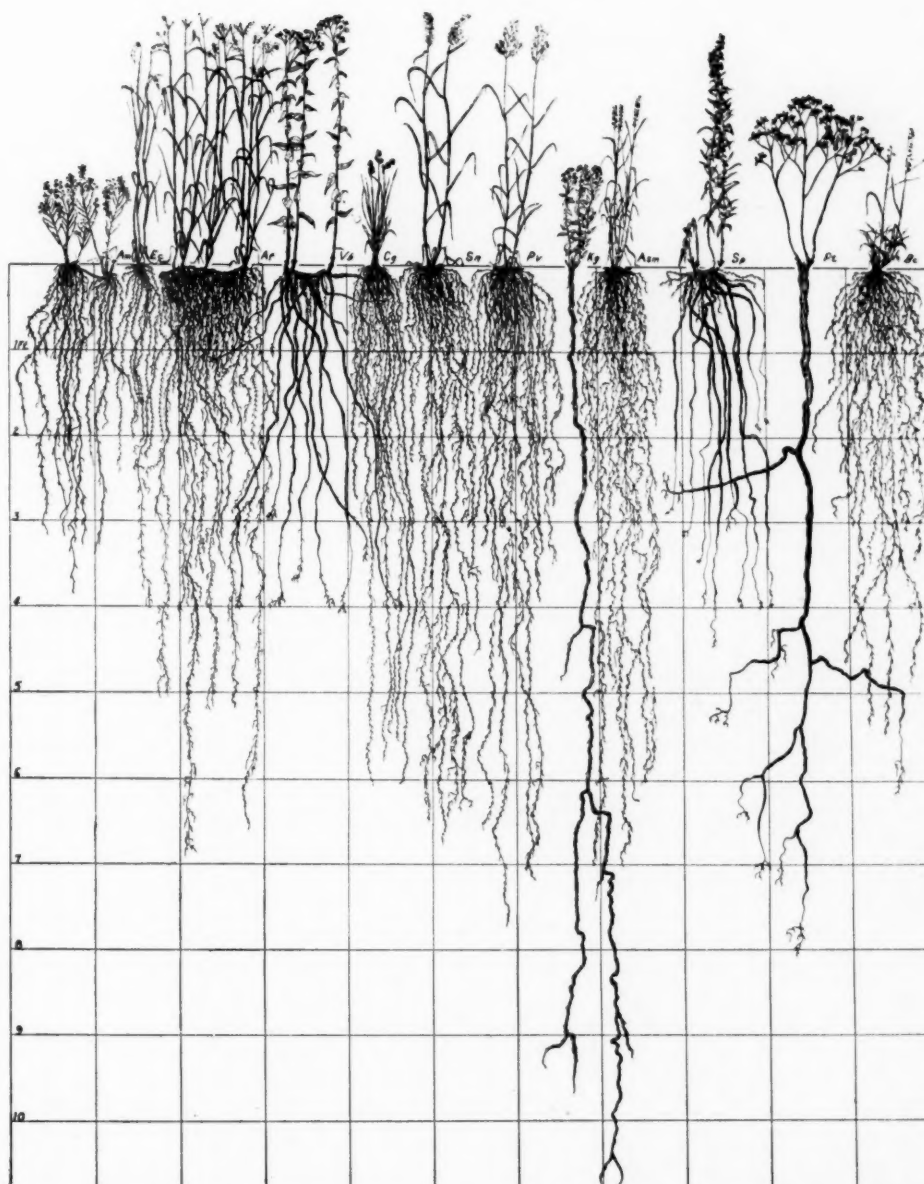


FIG. 40. Bisect showing relations of tops and roots of grasses and forbs typical of the big-bluestem type: *Aster multiflorus* (Am); *Elymus canadensis* (Ec); *Andropogon furcatus* (Af); *Veronia baldwini* (Vb); *Carex gravida* (Cg); *Sorghastrum nutans* (Sn); *Panicum virgatum* (Pv); *Kuhnia glutinosa* (Kg); *Agropyron smithii* (Asm); *Salvia pitcheri* (Sp); *Psoralea tenuiflora* (Pt) and *Bouteloua curtipendula* (Bc).

the taller ones. In the loess soils of the more gently rolling topography northward, for example, this condition prevails.

Andropogon scoparius, *A. nutans*, and *A. furcatus* often form more or less continuous irregular sodded areas varying from 6 inches to 7 feet in diameter where short grasses may be almost entirely excluded, while *Agropy-*

rum glaucum frequently occupies large areas rather exclusively. *Bouteloua racemosa* and *Elymus canadensis* are other important tall grasses. Alternating with these are similar or, on drier slopes, even larger areas of *Bulbilis dactyloides* and *Bouteloua gracilis*, intervening areas often to the extent of one-fourth of the surface being nearly devoid of vegetation. Perhaps more usually, however, the short and tall grasses are intimately mixed, the latter often showing strong tendencies toward the bunch habit. Carices . . . supplement the understory of grasses which reach an average height of about 4 inches as contrasted with the mid-summer tall-grass level 4 to 10 inches above (Weaver, 1924).

The deep soil of ravines and lowlands where rainfall is supplemented by run-in water affords a habitat where the tall grasses readily take complete possession. The short-grass layer cannot develop here because of the decreased light. This consociation is most nearly like the true prairie, although the more arid climate dwarfs all of the species in stature.

The shallow, open-textured soils of the steep slopes are so uncongenial to the sod-forming buffalo grass that it is practically absent. Likewise, blue grama is of little importance, although the tufts of hairy grama and certain sedges form a discontinuous understory on the upper slopes. Bunch grasses with their roots concentrated in the rock crevices thrive, as do also many deeply rooted forbs. The numerous bunch grasses and their associates, the upward spread of taller grasses from the ravines, and the intermingling of species from the short-grass areas of the uplands make this the most diversified consociation. Herbs of the early stages of the lithosere, not found elsewhere, characterize limestone outcrops, but deeply rooted forbs of medial or climax stages are found among them, absorbing far below in the deep crevices of the rock.

The short-grass uplands have the characteristic soil found westward in the "hard lands" of Colorado. But here the carbonate layer is much deeper. Extensive studies, including similar areas that have not been pastured for 16 to 20 years, reveal that the vegetation described for the uplands is typical. The poor development of the upper layer of mid grasses may have resulted from previous long periods of close grazing. The grouping (faciation) of *Bulbilis dactyloides* and *Bouteloua gracilis* on almost equal terms is common throughout the central portion of the mixed prairie (Clements, 1936).

The death of little bluestem by drought where it was intimately associated with big bluestem which survived seems, at first, paradoxical. The clue is found in the greater depth of rooting of the survivor. When soil moisture was exhausted to 3.5 to 4 feet, little bluestem perished. At this time big bluestem was absorbing from the 4- to 6-foot level (cf. Nedrow, 1937). *Bouteloua curtipendula* revealed a high degree of drought resistance. *Agropyron smithii* was a second species that increased its territory as a result of the drought.

In the study of underground parts, one of the chief impressions was the great advantage exhibited by the abundant, fine, minutely branched and

widely spreading roots of the grasses, especially of the uplands. In contrast, the root systems of most of the forbs would seem inefficient competitors when absorbing in the same soil area. In fact, forbs with roots confined to the grass-root zone usually mature early while water is normally plentiful. Others depend to a large degree upon soil moisture that is available beyond the root extent of the grasses. This is well portrayed in the bisects (Figs. 22, 34, 40).

The root habits of the grasses are similar to those described for true prairie (Weaver, 1919, 1920). Both little and big bluestem, however, were more shallowly rooted in the bunch-grass habitat on the rocks than elsewhere. This was true also of the other grasses and many forbs as well. Despite the reduced root depth, which apparently was due in part to the rocky substratum, water was normally sufficient for good growth. In fact, the wetness of the clay may itself have been a factor in retarding root elongation. The greatest depth attained by the grasses was in the deep alluvial soil of ravines. But even here *Panicum virgatum*, the most deeply rooted grass examined, was only 7 feet deep. In true prairie it reaches depths of 9 to 10 feet.

A group of shallowly rooted forbs, many others with tap roots that were little branched, and still others with generalized root systems adapted to absorb at all levels, show the several adaptations to the habitat. Various cacti and rather numerous other forbs, whose roots were examined but are not reported here, belong to one or the other of these classes. This is in agreement with the findings of other investigators of mixed-prairie species on "hard land." Weaver (1920) states:

Thus 11 per cent of the mixed-prairie species of hard lands are shallow-rooted, 28 per cent have little or no provision for surface absorption, while 61 per cent are both fairly deep-rooted and well adapted to absorb water even when the surface soil only is moist.

Compared to root depth in the more deeply moistened soils of true prairie, plants of mixed prairie are as a group more shallowly rooted. For example, *Aster multiflorus* extends to 3-4 feet as compared to 7-8 feet in true prairie. Comparative depths of the following species are: *Vernonia baldwini* 4 and 11 feet; *Salvia pitcheri* 4 and 8 feet; *Kuhnia glutinosa* 11-13 and 16-17 feet; *Lacinaria punctata* 4 and 16 feet; and *Amorpha canescens* 6-9 and 12-16 feet. This greater depth of penetration in the true prairie results from a deep, moist subsoil. It is of interest that under the still greater precipitation of Illinois where subsoil aeration becomes deficient, similar species again become less deeply rooted (Sperry, 1935).

The losses of water during the stress of great drought were higher than those determined during a 15-day period of somewhat typical weather at Phillipsburg, 70 miles due north. Weaver and Crist (1924) found by means of phytometers that *Bouteloua gracilis* and *Bulbilis dactyloides* each gave an average loss of one pound per square foot per day. The maximum at

Hays was 1.78 pounds. Losses from areas of *Andropogon furcatus* in the same sequence were 1.80 and 1.82 pounds per square foot, respectively. The big bluestem at Phillipsburg was much taller than that at Hays.

Among the many changes in plant populations resulting from the series of dry years none was more outstanding than the rapid reclaiming of the bared soil by buffalo grass. Blue grama grass has no such powers of vegetative propagation. Hence, from the nearly equal distribution of these two dominants in 1932, such great gains were made by the stoloniferous grass that by 1935 it was nearly twice as abundant as its codominant (Fig. 41).



FIG. 41. Stolons of *Bulbilis dactyloides* invading area left bare by the death of *Andropogon scoparius* and other grasses.

On the lowlands the losses of big bluestem have been largely replaced by the increase in slender grama grass and western wheat grass. Migration of blue grama grass from its stronghold in the clay soil near the bases of the hills into the tall-grass area was marked. Here it began to form a typical understory to the drought-weakened tall grasses, the dwarfed tops admitting sufficient light for growth of the smaller competitor.

Disappearance of the bunch grasses from the short-grass soil (except for remnants) was the most conspicuous change on uplands. It was here also that native forbs suffered the greatest losses and invasion by ruderals was most pronounced.

The marked increase in height of the dominants is of interest. The short grasses have a height of foliage of only 3 to 5 inches. That of little bluestem is 8 to 16. The height of the sod-formers of low ground is much greater, 12 to 20 inches. Of greater significance, however, is the ability of the short grasses to recover rapidly from drought-dormancy and make a renewed growth. In fact, they may ripen seed at any time from June to September. The taller grasses have no such adaptations. Development proceeds throughout the long season for growth, most of them flowering and fruiting in fall. Since little water is stored in soil and subsoil, lack of summer rainfall is a catastrophe especially to the taller grasses.

SUMMARY

The structure and distribution of three types of mixed prairie in west central Kansas have been determined and the factors controlling the distribution ascertained.

The rolling topography has resulted from the erosion of deep ravines through and beyond the thick, nearly horizontal layers of Fort Hays limestone.

Residual soil covers the rock 2 to 9 feet deep on the broad, nearly level uplands. Weathered limestone outcrops on the brows of the hills but is covered with about 2 feet of soil on the slopes. An exposure of shale near the base of the slopes has resulted in local strips of blue clay. Lower hillsides and ravines are covered with a thick mantle of eroded materials forming a deep soil.

The dark, silty clay loam of the uplands is a fine-textured, deep, fertile, residual soil with a mature profile. A distinct lime layer occurs at 25 to 38 inches and indicates the usual depth of soil moisture penetration. Shallow depressions near the periphery of the uplands are underlaid with a nearly impervious soil.

On the slopes the immature, dark gray, granular soil is porous, contains many fragments of limestone, but is only a few inches to 2 feet in depth. The underlying limestone, however, contains myriads of large fissures and crevices infiltrated with sandy clay.

The immature soil of the lowland is many feet in depth. This fertile, dark colored, granular, porous soil is high in silt and clay. Limestone fragments are common and layers of finely broken limestone pebbles occur below 4 feet.

Bulbilis dactyloides and *Bouteloua gracilis* in almost equal mixture clothe the nearly level uplands and recur on the impervious clay of lower slopes. A few species of mid grasses and numerous forbs of varying heights are scattered throughout.

The bunch-grass type of vegetation, dominated by *Andropogon scoparius*, covers the thin soils of the slopes. Numerous tall grasses and many forbs occur, the roots usually penetrating deeply into the rock crevices.

The moist lowlands are characterized by the tall and mid grasses of which *Andropogon furcatus* is dominant and *Bouteloua curtipendula*, *Agropyron smithii* and *Sporobolus drummondii* are important species. Numerous other tall grasses and coarse forbs abound.

The climate is semiarid. The long season for growth, an extremely variable annual precipitation averaging 22.8 inches and falling mostly as summer showers, high temperatures, low relative humidity, and much wind are the chief features.

Precipitation is extremely variable. During the years 1927 to 1932 inclusive it averaged 5 inches above the mean, and from 1933 to 1935 inclusive 7.5 inches below normal. This study was made during this latter period of drought.

Runoff from soil bearing short grasses is high since rate of percolation is low. Water percolates much more readily into soils bearing bunch grasses. This vegetation also benefits by the absorption of runoff water from the short-grass area. The deep soils of the ravines have the highest rate of water penetration. They receive much run-in water.

Water content of soil showed a close correlation with precipitation. There was often no available water in the surface foot of short-grass soil and during several extended periods each year this condition prevailed to a depth of 3 to 6 feet. The grasses underwent corresponding periods of dormancy.

Periods of extreme water shortage also occurred in the shallow soils of the bluestem habitat. Here the deeply rooted vegetation survived by absorbing from soil in the fissures and pockets of the rock.

Water was nearly always available to big-bluestem vegetation except late in 1935 when none was available at any depth to 5 feet, but this deficiency was of relatively short duration.

Normal daily maximum summer temperatures of 80° to 100°F. increased to 100° to 110°F. during the drought. Soil temperatures at 3 inches depth were correspondingly high.

Daily evaporation rates in the short grass fluctuated between 18 and 138 cc., rates of 75 to 100 cc. being common during drought. Evaporation in the little-bluestem habitat was 10 to 30 cc. less. A still further decrease of 5 to 20 cc. was measured in the big-bluestem habitat.

Winds, averaging 7 to 28 miles per hour, increased evaporation rate.

Water losses from phytometers of one square foot of each kind of vegetation were greatest in short grass and least in the big-bluestem type. Average losses of 1.2 to 1.8 pounds per square foot per day were usual.

Structure of the vegetation was studied by means of scores of permanent quadrats which were recharted once or more annually. Thus shiftings in plant populations resulting from drought were also determined. Trenches for root study were made in each community and often in the ecotone between communities.

Bulbilis dactyloides and *Bouteloua gracilis* each compose about 40 per cent of the short-grass type. Early growth in spring, the formation of a dense sod, early blossoming and fruiting, and rapid recovery from dormancy after drought characterize these grasses. Buffalo grass reclaims rapidly areas bared by drought.

The usual basal cover of short grasses is 70 to 90 per cent but this decreases to 20 to 30 per cent in shallow depressions where nearly impermeable subsoil occurs.

Andropogon scoparius, *Aristida purpurea*, certain other mid grasses and the less xeric forbs suffered great losses by drought in areas where the short grasses were little harmed.

Root penetration of the buffalo grass and blue grama grass is about 5 feet. Numerous forbs are similarly or more shallowly rooted; a few penetrate deeper, some to 9 feet. The soil is well occupied by underground parts.

Andropogon scoparius dominates the steep hillsides characterized by bunch grasses. *Sporobolus pilosus* and *Bouteloua hirsuta* are its chief associates on the brows of the hills and *Andropogon furcatus*, *Bouteloua curtipendula* and *Panicum virgatum* in deeper soils.

Little bluestem alone affords more than 70 per cent of the vegetation. Thirty per cent or less of the soil is covered on the brows of the hills, but elsewhere the basal cover varies between 40 and 60 per cent.

A greater number of species and better developed societies of forbs occur in the bunch grass than in either the drier short-grass habitat or the less xeric lowland dominated by tall sod-forming grasses.

During normal years the vegetation is 12 to 16 inches tall by midsummer.

Early blooming forbs are usually shallowly rooted. Little bluestem and other grasses penetrate the soil and clay-filled crevices to 3 or more feet. Certain important long-lived forbs extend their roots downward 4 to 6 feet on south slopes and 6 to 12 feet in the deeper soils of north-facing ones.

A relationship was determined between depth of rooting and resistance to drought among several related species.

Andropogon furcatus dominates low ground where runoff water and blown-in snow from the slopes augment the precipitation. It composes 75 per cent of the vegetation. With *Bouteloua curtipendula*, *Panicum virgatum* and other sod-forming grasses it forms an almost continuous cover. Big bluestem is very uniformly distributed.

The general level of the vegetation is about 18 inches in midsummer before the development of flower stalks.

Agropyron smithii, because of deficient rainfall, has increased greatly in the big bluestem consocieties during the period of investigation.

A lower story of *Poa arida* and mostly early blooming forbs occurs below the grasses and a more pronounced one of midsummer and autumnal blooming forbs above them. This type most nearly approaches true prairie in appearance and structure.

Roots of the grasses thoroughly occupy the soil to a depth of 4 to 7 feet. They are somewhat coarser but much deeper than those of the short grasses. Certain forbs are more shallowly rooted than the grasses; others extend to greater depths.

Distribution of the three types of mixed prairie vegetation is clearly correlated with topography and especially with the soil environment. Water content is the controlling factor.

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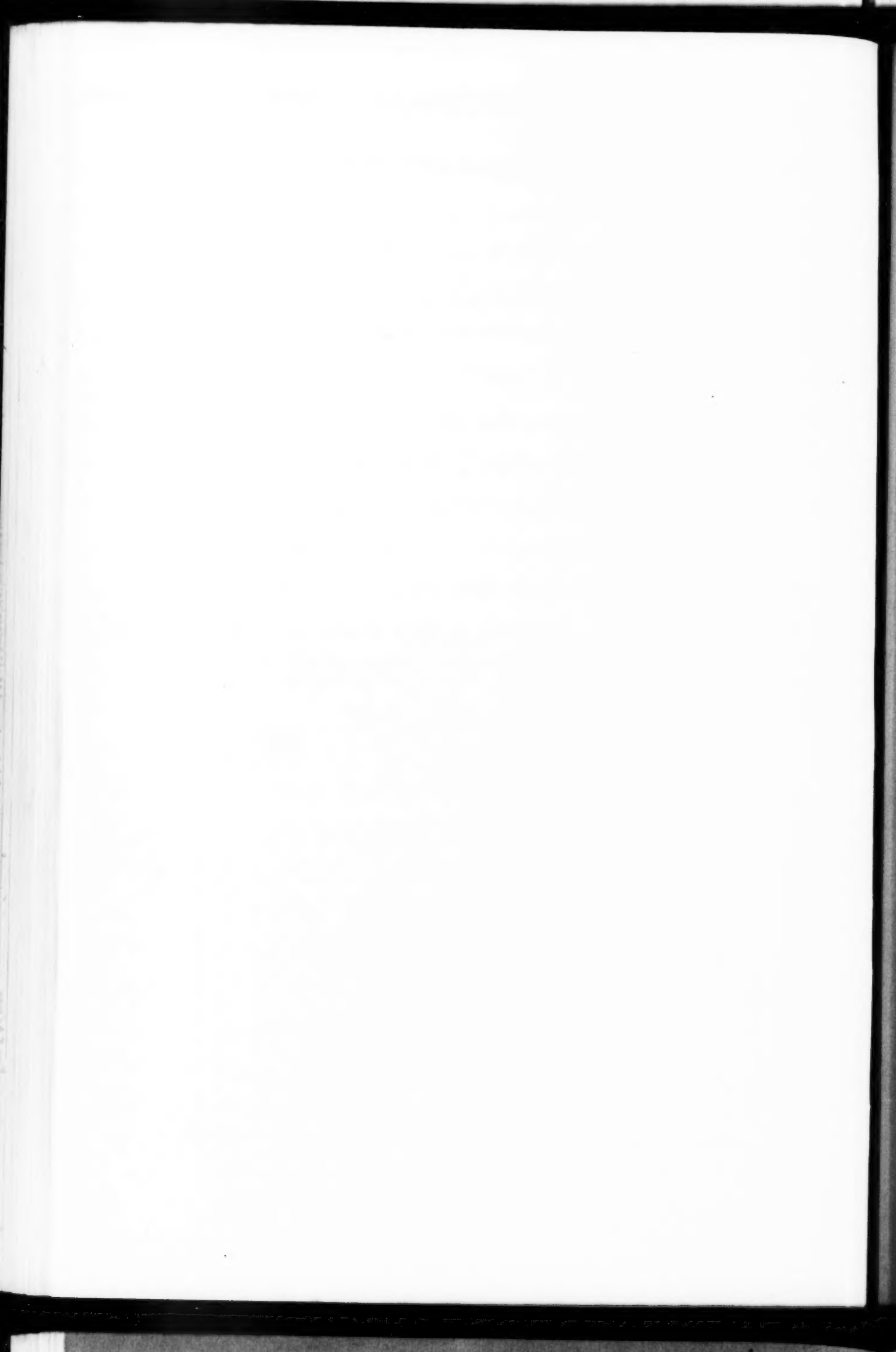


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